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Species Diversity, Phenology, and Temporal Flight Patterns of *Hypothenemus* Pygmy Borers (Coleoptera: Curculionidae: Scolytinae) in South Florida

Andrew J. Johnson,[1] Paul E. Kendra,[2,3] James Skelton,[1] and Jiri Hulcr[1,4]

[1]School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611 (andrewjavanjohnson@gmail.com; skelto3@gmail.com; hulcr@ufl.edu), [2]USDA-ARS, Subtropical Horticulture Research Station, Miami, FL 33158 (paul.kendra@ars.usda.gov), [3]Corresponding author, e-mail: paul.kendra@ars.usda.gov, and [4]Entomology and Nematology Department, University of Florida, Gainesville, FL 32611

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Abstract

Hypothenemus are some of the most common and diverse bark beetles in natural as well as urban habitats, particularly in tropical and subtropical regions. Despite their ecological success and ubiquitous presence, very little is known about the habits of this genus. This study aimed to understand species diversity and daily and seasonal trends in host-seeking flight patterns of *Hypothenemus* in a suburban environment by systematic collections with ethanol baiting over a 15-mo period in South Florida. A total of 481 specimens were collected and identified as eight species, most of them nonnative. *Hypothenemus* formed the overwhelming majority of bark beetles (Scolytinae) collected, confirming the dominance of the genus in urban environments. *Hypothenemus brunneus* (Hopkins) and *Hypothenemus seriatus* (Eichhoff) were most abundant, comprising 74% of the capture. Rarefaction showed that the sample was sufficient to characterize the local diversity and composition. The seasonal pattern in *Hypothenemus* capture was positively correlated to day-time temperature, not to season as in most temperate Scolytinae. Another significant observation in the community dynamics was the synchronized occurrence of two common species (*H. birmanus* and *H. javanus*), unrelated to season. *Hypothenemus* were predominantly diurnal with a broad flight window. Females flew as early as 11:00 hours (EDST), with peak flight occurring at 15:00 hours, significantly earlier than flight patterns of most other Scolytinae. Surprisingly, male *Hypothenemus* were frequently collected, despite their lack of functional wings. Several potential explanations are discussed. This is the first study into the ecology of an entire community of the twig-feeding *Hypothenemus*.

Key words: bark beetle, phenology, diversity, diurnal, circadian

Bark beetles in the genus *Hypothenemus* (Coleoptera: Curculionidae: Scolytinae: Cryphalini) are common and species rich in tropical and subtropical areas worldwide. There are 22 species known from Florida (Johnson et al. unpublished) , of which five are thought to be nonnative (Wood 1982). They are functionally haplo-diploid (Vega et al. 2015) and live subsocially. Many species are broad generalists, able to reproduce successfully on a wide range of plant host families. Most live within twigs, feeding on dead and dying plant material, but two species have become notorious pests of seeds—the coffee berry borer, *Hypothenemus hampei* (Ferrari), and the tropical nut borer, *Hypothenemus obscurus* (F.). Due to their ecological versatility, several species are distributed globally, including in urban habitats, and *Hypothenemus* is the most commonly intercepted genus of Scolytine beetles at U.S. ports (Haack 2001).

Members of the genus *Hypothenemus* have been rarely studied, likely due to their minute size (adults are typically <2 mm in length) and difficulties with their identification. This is despite their incredible abundance and fascinating life history. The only well-studied species is the coffee berry borer, *H. hampei*. In this species, females fly in the late afternoon and early evening hours, and are highly attracted to ethanol, which provides the basis for effective pest detection (Vega et al. 2015). Other *Hypothenemus* species are usually collected as chance encounters, the by-catch from trapping efforts directed at other Scolytinae, or from inspections at ports of entry. There are virtually no studies on the basic natural history and ecology of the overwhelming majority of this diverse, wide-spread, and potentially economically important group.

To gain a better understanding of the *Hypothenemus* community in a subtropical urban habitat, a survey was conducted in a

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residential area in Broward County, South Florida. The main focus was to collect information on the diversity and relative abundance of *Hypothenemus* species, and also to document seasonal and daily flight patterns. With collections on 90 sampling dates over a period of 15 consecutive months, and with species-level resolution, this is the most extensive published study on the ecology of this genus.

Materials and Methods

Site Description

The study site consisted of a heavily landscaped private residence (2023 m^2) in Plantation, FL (Broward County; 26° 06′996″ N, 80° 16′355″ W), typical of a middle-class suburban environment in the Greater Ft. Lauderdale area. There were adjoining residential properties to the north and south, an open golf course to the east, and a tennis court and fresh water pond to the west. Beetle collections were conducted on a shaded brick patio. The vicinity included a diverse assemblage of potential woody hosts, most of them nonnative ornamentals, dominated by an overhanging Hong Kong orchid tree (*Bauhinia* 'Blakeana' Dunn), and also including mango (*Mangifera indica* L.), orange (*Citrus sinensis* (L.) Osbeck), Jacaranda (*J. mimosifolia* Don), live oak (*Quercus virginiana* L.), silk floss kapok (*Ceiba speciosa* (A. St.-Hil.) Ravenna), ylang-ylang (*Cananga odorata* (Lam.) Hook. F. & Thomson), weeping fig (*Ficus benjamina* L.), Cassia (*C. surattensis* Burm.f.), firebush (*Hamelia patens* Jacq.), and Clerodendrum (*C. quadriloculare* (Blanco) Merr., and *C. speciosissimum* Drapiez). There were also various palms of seed-bearing age, including Montgomery (*Veitchia montgomeryana* H.E. Moore), adonidia (*V. merrilli* (Becc.) H.E. Moore), Carpentaria (*C. acuminata* (H.A. Wendl. & Drude) Becc.), coconut (*Cocos nucifera* L.), Chinese fan (*Livistona chinensis* (Jacq.) R.Br. ex Mart.), and queen (*Syagrus romanzoffiana* (Cham.) Glassm.).

Collection Method

In previous research using host wood and essential oil lures (which released high levels of the same host-based kairomones) as bait for collection of redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff, it was observed that other Scolytinae were also attracted, including *Hypothenemus* (Kendra et al. 2012a,b). Therefore, this baiting method was adopted as a sampling technique for detection of *Hypothenemus*, but simplified by using only ethanol, a more effective attractant for this group (Kendra et al. 2014b, Vega et al. 2015). A white cotton sheet was spread at the collection site and a single ethanol lure ("Ultra high release" lure, Contech Enterprises, Inc., Victoria, BC) was suspended from a tripod 1 m above the sheet. This lure consisted of a black plastic tube, 30.5 cm in length and 3.8 cm in diameter, which likely provided a visual cue as well. At hourly intervals, the sheet was inspected for beetles, which were collected by hand with a soft brush and immediately placed into 95% ethanol. Occasionally, beetles were observed hovering above the sheet, in which case they were batted down gently prior to collection. After each inspection, the lure was shaken vigorously to generate an attractive pulsed plume of ethanol vapor. In September 2013, preliminary observations were made over a 24-h period to identify the general circadian flight pattern of female *Hypothenemus*. Thereafter, collections were conducted from ∼10:00–20:00 hours (EDST), with a total of 90 collections made over a 15-mo period from October 2013 through December 2014. Data recorded in the field consisted of the number of *Hypothenemus* (and other Scolytinae) caught and the time of each capture. Preserved specimens were then shipped to the University of Florida (Gainesville) for morphology-based identification by A.J.J.

Statistical Analysis

Flight patterns were analyzed using a regression of the time of day and the number of in-flight *Hypothenemus* collected (Systat Software 2010). Pearson product moment correlation (Systat Software 2010) was used to compare mean beetle captures each month with mean monthly maximum and minimum temperatures. Temperature data were obtained from the National Climatic Data Center, National Oceanic Atmospheric Administration, via their website (http://www.ncdc.noaa.gov/, last accessed August 2015). Values were those recorded at the Fort Lauderdale-Hollywood International Airport, located ∼19 km east of the collection site.

Seasonal flight patterns were examined using generalized additive models (GAM) and principal coordinate analysis (PCoA) of the relationship between sampling date and *Hypothenemus* community composition. *Hypothenemus* collections were binned by month of collection for the sampling period. Monthly samples were then used to generate a pairwise Bray Curtis distance matrix using the vegdist() function in the Vegan package for R, v 2.3.1 (Oksanen et al. 2011). Principal coordinates analysis ordination on the Bray Curtis distance matrix was conducted using the pcoa() function in the ape package for R, v. 3.3 (Paradis et al. 2004). The first principal coordinate was regressed against study month (as an integer value from 1 to 15) using a generalized additive model with a Gaussian error distribution, gam() function in the mgcv package for R, v 1.8-7 (Wood 2011). After a significant effect of sampling month on aggregate species composition was established, post hoc analyses were performed for each beetle species to characterize the observed change in species composition. For each species, a GAM was used to regress relative abundance against sampling month, assuming a binomial error distribution. Validation of error distributions and default basis dimensions were assessed visually by scatterplots comparing fitted values to raw data, predicted values and residuals, histograms of residuals, and permutations test for basis dimensions implemented by the function gam.check(), in the mgcv package for R, v 1.8-7 (Wood 2011).

The completeness of our sampling effort and the total local diversity of *Hypothenemus* collectable by ethanol baiting was estimated by interpolation and extrapolation sampling curves of Hill numbers (species richness and Simpson diversity) following the methods of Chao et al. (2014). Sampling curves were generated using the iNEXT() function in the iNEXT package for R, v 2.0.5 (Hsieh et al. 2013). Sampling curves were calculated for species richness ($q = 0$) and for Simpson's diversity ($q = 2$) and extrapolated to double the actual sample size. Diversity estimates and 95 % confidence intervals were calculated at 100 knots, using 100 bootstrap replications per knot.

Results

Collection of live beetles with ethanol baiting yielded 481 specimens of *Hypothenemus*, representing eight species (Table 1). The two most abundant were *H. brunneus* (Hopkins) and *H. seriatus* (Eichhoff); these two species comprised 74% of the captures. *Hypothenemus crudiae* (Panzer) and *H. setosus* (Eichhoff) were the least common, each encountered only twice during the 15-mo survey. Interestingly, collections also included males of the two dominant species, *H. brunneus* (10 specimens) and *H. seriatus* (1 specimen). The sampling method was highly effective for attraction

Table 1. Number of *Hypothenemus* (Coleoptera: Curculionidae: Scolytinae) collected in a 15-mo survey conducted in Plantation, FL (Broward County)

Month (No. of collection days)	Species							
	H. birmanus (Eichhoff)	*H. brunneus* (Hopkins)	*H. columbi* Hopkins	*H. crudiae* (Panzer)	*H. eruditus* Westwood	*H. javanus* (Eggers)	*H. seriatus* (Eichhoff)	*H. setosus* (Eichhoff)
2013								
Oct. (6)	2	3			5	2	10	
Nov. (8)	5	5			4	9	17	
Dec. (6)	3	6	4		1	7	11	
2014								
Jan. (2)	3	5				2	1	
Feb. (6)	3	6			1	1	7	
Mar. (5)	6	9			4		3	1
April (5)	4	9		1	1	3	2	
May (7)	2	6	2		1	6	8	
June (2)		4			3		1	
July (9)	1	27 (2♂)			3	1	35 (1♂)	
Aug. (7)		18 (3♂)	1	1	10	2	35	
Sept. (6)	1	28 (1♂)			1	1	17	
Oct. (7)		17 (1♂)	2		3	1	25	1
Nov. (5)		7 (1♂)			5		15	
Dec. (9)		8 (2♂)	1		3	1	11	
Total (90)	30	158	10	2	45	36	198	2

Unless noted otherwise, values indicate number of females.

of *Hypothenemus*, which made up 97% of the total beetle captures. Only two nontarget Scolytinae were observed at the study site—*Xylosandrus compactus* (Eichhoff), tribe Xyleborini (8 specimens) and *Coccotrypes* spp., tribe Dryocoetini (7 specimens). In addition, one bostrichid beetle was collected.

The survey provided no evidence of seasonal presence or absence of *Hypothenemus*, with most species detected throughout the year in South Florida. However, highest numbers of beetles were observed during the late summer and early fall of 2014 (Fig. 1A). This pattern of peak abundance in *Hypothenemus* followed a seasonal increase in ambient temperature (Fig. 1B), and numbers collected were positively correlated with mean monthly maximum (*Pearson coeff.* = 0.604, $P = 0.017$) and minimum (*Pearson coeff.* = 0.553, $P = 0.033$) temperatures.

Sampling curves revealed that our sampling effort ($n = 481$) was beyond the asymptote for species richness ($q = 0$) and Simpson diversity ($q = 2$), and therefore sufficiently characterized the diversity of *Hypothenemus* susceptible to our ethanol-based collection methods (Fig. 2). Although we found no evidence of seasonality in the community as a whole, *Hypothenemus* species composition changed significantly during the sampling period. Individual species followed specific patterns, but in no case do these appear to correlate with seasons. Principal coordinate analyses of monthly samples captured 31% of the variation in species composition in the first principal coordinate (PCo1). Subsequent principal coordinates each captured < 20% of variation and were not further analyzed. GAM regression showed a significant relationship between sampling month and PCo1, largely driven by an abrupt shift in species composition between May and June of 2014 (Fig. 3; $F = 8.257$, $P = 0.006$, adj $R^2 = 0.823$). Post hoc analyses revealed significant temporal changes in the relative abundances of three *Hypothenemus* species; decreases in the relative abundance of both *H. birmanus* ($\chi^2 = 18.44$, $P < 0.001$, adj $R^2 = 0.843$) and *H. javanus* ($\chi^2 = 18.71$, $P < 0.001$, adj $R^2 = 0.460$) during early summer of 2014, and an increase in *H. brunneus* ($\chi^2 = 7.533$, $P < 0.05$, adj $R^2 = 0.358$). The abrupt shift in

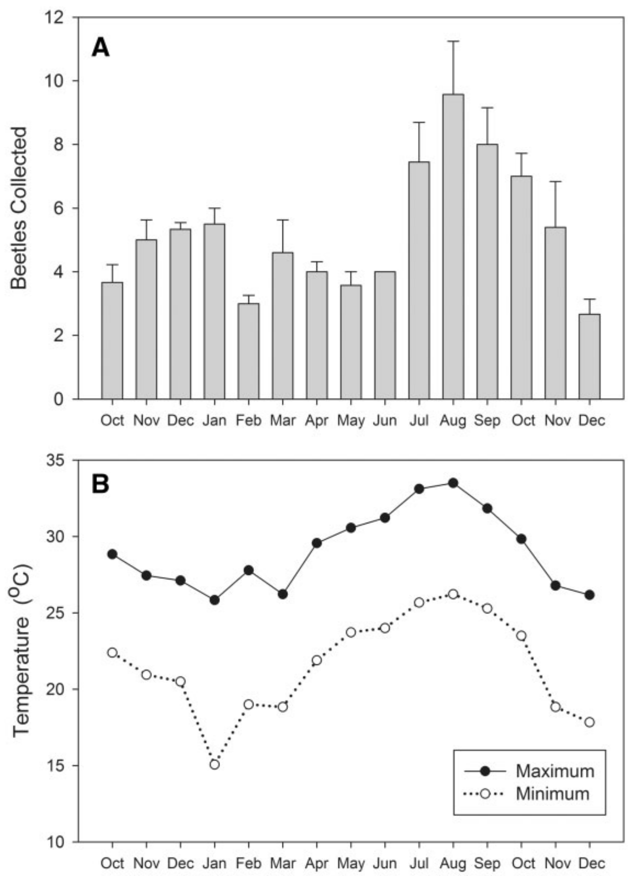

Fig. 1. Seasonal flight patterns of the aggregated *Hypothenemus* community. Mean (±SE) number of beetles collected per sampling date (**A**) and mean maximum and minimum temperatures (**B**) for each month of a 15-mo survey conducted in Broward County, FL (2013–2014). Temperature data were obtained from the National Climatic Data Center, NOAA.

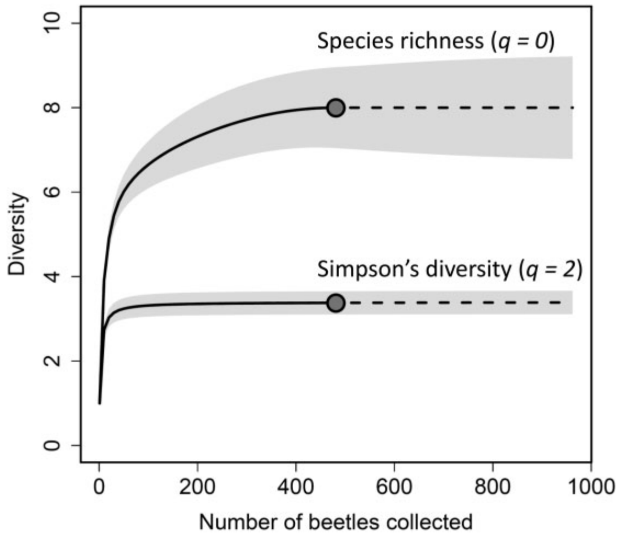

Fig. 2. Sampling curves drawn from interpolation and extrapolation of Hills numbers for observed species richness (q = 0) and Simpson's diversity (q = 2) of *Hypothenemus* species collected over the duration of the study. Interpolated (solid lines) and extrapolated (dashed lines) estimates of species richness and diversity are plotted against sample size (number of beetles collected). Gray area represents 95% confidence of 100 bootstrap replicates across 100 knots. Dark gray circles show actual sample size.

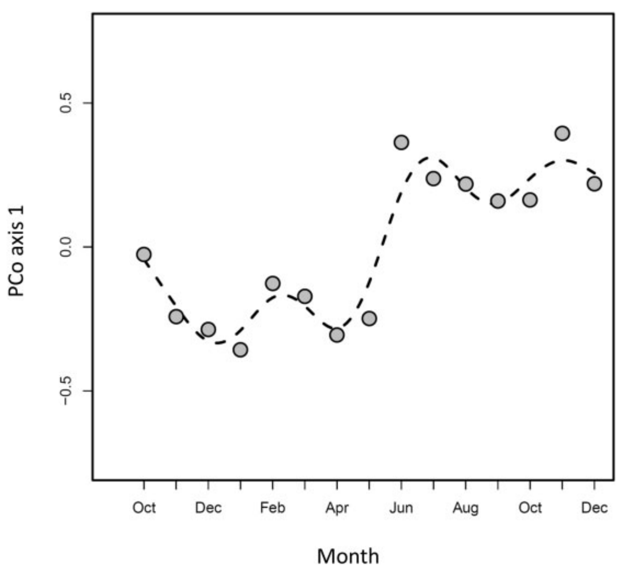

Fig. 3. Change in *Hypothenemus* composition over course of survey. Composition is represented by the first principal coordinate of a Bray Curtis dissimilarity matrix (gray symbols). Dashed line represents generalized additive model (GAM) fit.

community composition identified by GAM regression of PCo1 coincided with decreases in the relative abundances of *H. birmanus* and *H. javanus* during early summer of 2014 (Fig. 4).

A broad flight window was documented for female *Hypothenemus* (Fig. 5). Beetles were observed flying as early as 11:00 hours, with peak flight occurring around 15:00 hours. There was a sharp decline in numbers after 17:00 hours, with no females collected after ∼19:30 hours. This pattern fitted well to regression with a Gaussian peak model ($y = 6.91e^{-0.5[(x\text{-}1488.66)/252.39]3.9}$, $R^2 = 0.977$).

Discussion

An ethanol lure suspended above an out-stretched white cotton sheet was found to be a simple, yet highly effective method for collection of *Hypothenemus*. This complements field observations by A.J.J. (unpublished data) of *Hypothenemus* flying near ethanol-baited traps, but not getting close enough to be captured. It is also consistent with observations made while baiting for *X. glabratus* (Kendra et al. 2015a): females frequently flew close to the bait (essential oil lures or host *Persea* wood), but then landed on the sheet 0.5–1.0 m away and proceeded to walk toward the bait. With both taxa, these observations suggest that, in addition to semiochemcials, visual cues are important in the host location process (Kendra et al. 2014a).

Further support for utilization of visual cues by *Hypothenemus* is provided by the diurnal flight patterns documented in this study. In previous investigations conducted in North Florida (Alachua, Marion Counties), Central Florida (Highlands, Glades Counties), and South Florida (Miami-Dade County), the majority of Scolytine beetles, including species sympatric with *Hypothenemus*, were observed to initiate flight in late afternoon and peak near sunset, 20:00 hours EDST (Kendra et al. 2011, 2012a, b, 2014b, 2015a). In contrast, in-flight females of *Hypothenemus* were observed in late morning, peaked during the mid-afternoon hours, and then declined sharply after 17:00 hours (several hours prior to sunset). To the authors' knowledge, the only other scolytines in Florida that have comparable diurnal flight windows are *Xyleborus glabratus* (peak flight at 18:30 hours; Kendra et al. 2012a) and *Xyleborinus andrewesi* (Blandford) (peak flight at 17:00 hours in Highlands County; P.K. unpublished data), and there is experimental evidence that the former species uses stem diameter as a visual cue for optimal host location (Mayfield and Brownie 2013). These species-specific flight windows should be accounted for when surveying the Scolytinae of a given area, or when considering control strategies for pest species.

In addition, engaging in host-seeking flight when there is ample daylight may allow female *Hypothenemus* to assess the sun exposure of the substrate (small twigs), which is an indirect indicator of moisture content. Substrate moisture content is important for most generalist bark and ambrosia beetles, and diurnal flight may allow for better assessment of host conditions before committing to gallery excavation. At least for the coffee berry borer, after a gallery is initiated, the wing muscles of the founding female degenerate (López-Guillén et al. 2011), preventing further flight to search for an alternate site, should conditions become unfavorable.

Very few *Hypothenemus* are plant host specialists. The only two known from South Florida are *H. pubescens* Hopkins and *H. parvistriatus* Wood, which feed on coastal grasses and ferns, respectively (Wood 2007). Neither was collected in this study. This may have been the result of a lack of available hosts near the collection site, or insufficient attraction of ethanol for these host-specific bark beetles.

Encountering males while trapping for host-seeking females was an unexpected outcome, reflective of our poor understanding of this genus beyond the well-known pest species. It has been assumed that all males of *Hypothenemus* have habits and morphological characteristics similar to those of the coffee berry borer. Sexual dimorphism is pronounced in the coffee berry borer; males are much smaller than females, short lived, unable to fly, and have little or no visual acuity (Vega et al. 2014). It has also been assumed that these feeble males never leave their gallery, mating only with their siblings. Our observations challenge some of these current assumptions. Although males of the majority of North American species have vestigial wings, are smaller, and possess fewer ommatidia than

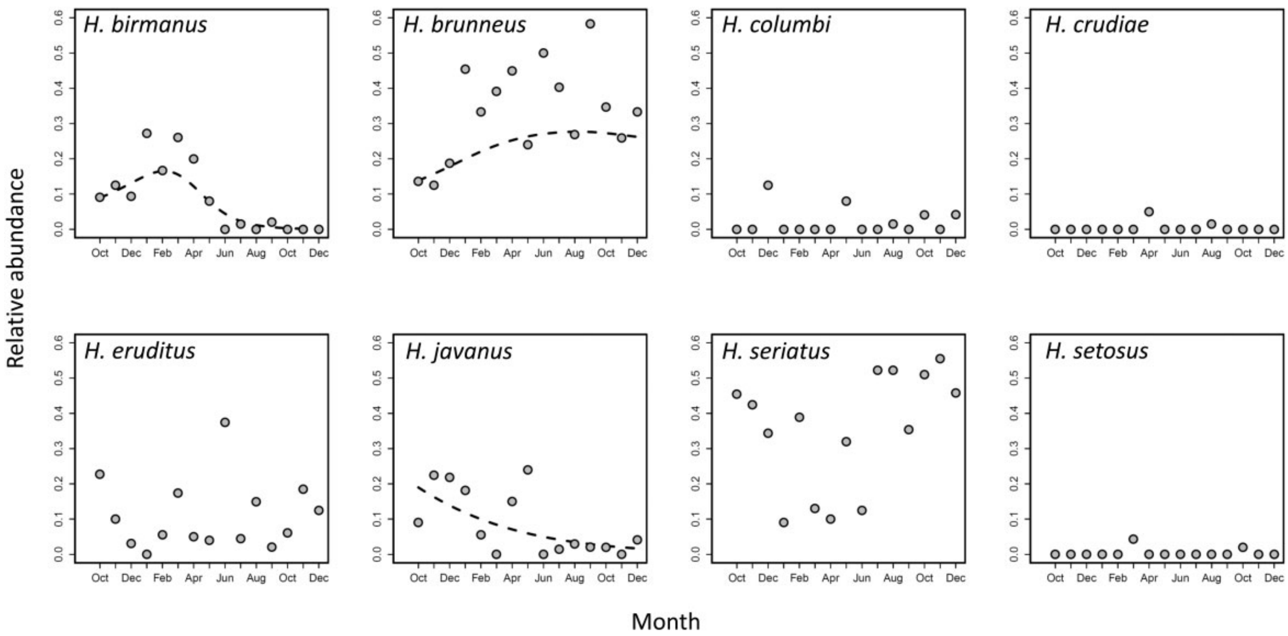

Fig. 4. Species-specific changes in relative abundance over the course of survey. Relative abundance is shown as the proportion of all individuals represented by each species. Generalized additive model (GAM) fit is shown as dashed line for species found to change significantly over the course of the study.

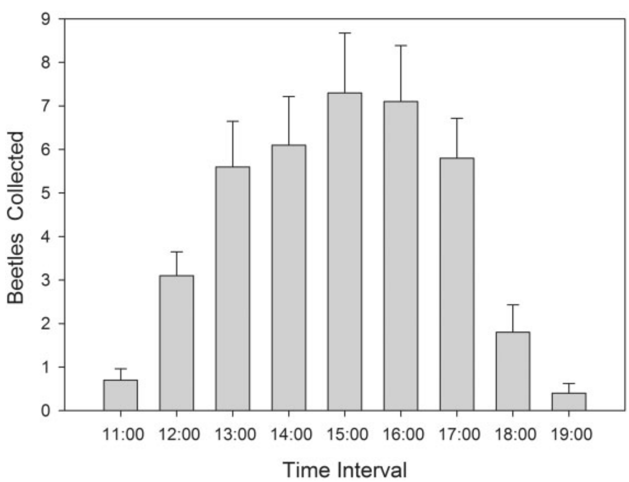

Fig. 5. Daily flight patterns of female *Hypothenemus.* Mean (±SE) number of beetles collected per month, recorded at hourly intervals from 10:00 to 20:00 hours, in a 15-mo survey conducted in Broward County, FL (2013–2014). Labels on the x-axis specify the starting time of each 1-h collection period (all converted to EDST).

females, the males of *H. brunneus* we collected were robust and almost as large as females. This may be adaptive for leaving the gallery, as we observed in this study. It is not clear whether the males were attracted to the ethanol vapor (a kairomone) or to the females (a potential source of pheromones), or just passively found their way onto the sheet (e.g., fell from the overhanging *Bauhinia* tree). It is also possible, though not likely for *H. brunneus*, that small males can travel phoretically on females.

With the trapping method reported here, there were surprisingly few other Scolytines collected in this urban habitat compared with forested sites elsewhere in Florida (Kendra et al. 2015a, b; Steininger et al. 2015). This may have been the result of scant availability of dead host material in the well-maintained residential community, except for small branches and seeds suitable for colonization by *Hypothenemus*. Alternatively, this observation may suggest that *Hypothenemus* thrive in the urban landscape where other generalist bark and ambrosia beetles do not. Most *Hypothenemus* species encountered were nonnative, and all but one (*H. columbi*) are widely distributed species abundant outside their original range, almost certainly the result of increased global commerce. Many species also colonize twigs killed by the black twig borer, *Xylosandrus compactus*, which was detected at the study site. Since *X. compactus* and most of these *Hypothenemus* are nonnative, the situation fits the "invasion meltdown" hypothesis, in which exotic species facilitate each other's success in a nonnative region (Simberloff and Von Holle 1999). It is also worth noting that a test deployment of the same trapping method in North-central Florida (Gainesville), yielded an almost entirely different assemblage of species, including *H. dissimilis*, *H. interstitialis*, *H. seritatus*, and *H. eruditus* (unpublished data). All these species are native to Florida. South Florida may be much more prone to invasion and successful establishment of exotic *Hypothenemus* species due to its climate and abundance of nonnative woody ornamentals, or perhaps the more temperate species are simply not competitive in subtropical ecosystems.

Temporal trends observed over the course of this study suggest that the total abundance of all species of dispersing *Hypothenemus* is highly seasonal and largely dependent on temperature. In contrast, the species composition of dispersing *Hypothenemus* can vary considerably through time but is not seasonal. There was a shift in species composition between May and June of 2014 that reflected a pronounced decline in the relative abundances of two common species, *H. birmanus* and *H. javanus*. Prior to May 2014, these two species comprised approximately a third of beetles collected in each month, but they were rare or absent in collection beyond May 2014. Thus, the observed shift in *Hypothenemus* species composition could reflect synchronized boom and bust population dynamics of those two species; however, the underlying driver of those dynamics remains unknown. Together, the results of our analyses suggest that *Hypothenemus* species vary independently in their dispersal phenology. Specifically, most or all populations of dispersing *Hypothenemus* are more abundant during warm parts of the year, whilst populations respond independently to factors other than seasonal temperature variation. This result is congruent with the vast taxonomical and ecological diversity of this group, and begs for future efforts to uncover the underlying factors that drive species-specific dynamics of *Hypothenemus*.

We used a morphological species concept, even though we understand that there may be a degree of cryptic diversity among our samples. Studies on cryptic bark beetles which use molecular markers frequently find high level of genetic variation within a species. The genetic diversity of *H. eruditus* in Panama has been found to be as high as 20.1% in a part of a mitochondrial gene (COI) (Kambestad 2011), which would typically suggest the presence of very divergent cryptic species. However, it is not clear whether the inbred mating system accounts for the high genetic variation, and whether the traditional species concepts can even be applied to inbreeding species.

This study is still the first which uses identified *Hypothenemus* in an ecological context, and reports patterns between the species that comprise a subtropical bark beetle community. The flight patterns and ethanol-baiting collection method used in this study will be invaluable for further study and efficient detection of *Hypothenemus* species, the most common bark beetles in residential areas in the tropics and subtropics.

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