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Distribution of *Phloeosinus tacubayae* Hopkins, 1905 (Curculionidae, Scolytinae), the Cypress Bark Beetle, and new records from potential distribution models

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Abstract

We evaluated the biotic and abiotic conditions related to the presence of *Phloeosinus tacubayae* Hopkins, 1905, to update its distribution and explore new areas to collect the species from potential distribution models and establish its host range. Our results support that *P. tacubayae* is an oligophagous species distributed mostly in five provinces from the Mexican Transition Zone; its distribution pattern belongs to the Nearctic cenocron and is related to the distribution pattern of its principal host. The modeling and distribution of its hosts suggest invadable zones where new records may exist.

Keywords

Geographic range, maximum entropy, Mexican biogeographic provinces, Nearctic cenocron

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Introduction

The members of *Phloeosinus* Chapuis, 1869 are bark beetles that feed and reproduce mainly on conifers of the family Cupressaceae (Atkinson et al. 1986; Pfeffer 1995). Due to the construction of their gallery systems, their host plants lose vigor, weaken physiologically, lose their ornamental appearance, and finally die. Therefore, these insects are elements that promote the regeneration of natural forests (Faccoli and Sidoti 2013). Most species are classified as early successional saprophagous, but when their populations are high, some species are aggressive and cause considerable tree mortality and, thus, can be pests in natural and urban settings (Craighead and George 1930; Fettig 2016).

Currently, *Phloeosinus* includes 80 described species, of which more than 66 are taxonomically valid. They are mainly distributed in the Nearctic and Palearctic regions (Faccoli and Sidoti 2013; Kirkendall et al. 2015). Almost 50% of them, 26 species and four subspecies, inhabit North and Central America (Atkinson 2022). Cypress Bark Beetle, *Phloeosinus tacubayae* Hopkins, 1905, is a native to Mexico and Central America (Wood 1982; Atkinson et al. 1986), with most of its records from the Mexican Transition Zone (Atkinson 2018). This species inhabits coniferous, oak, mountain mesophytic, and tropical deciduous forests (CONAFOR 2017). It develops mosts of its life cycle in the Mexican Cypress, *Hesperocyparis lusitanica* (Mill.) Bartel (= *Cupressus lusitanica* Mill., *C. lindleyi* Klotzsch ex Endl., *C. lusitanica var. lindleyi* Klotzsch ex Endl.), but there are also a couple of records from Arizona Cypress, *Hesperocyparis arizonica* (Greene) Bartel (Atkinson and Equihua 1985). Most of the geographic records of *P. tacubayae* have been reported from *H. lusitanica*. [All native species of *Cupressus* L. distributed in the Americas are now included in *Hesperocyparis* Bartel & R.A. Price based on morphological and molecular evidence following Adams et al. (2009) and Terry et al. (2012, 2016)]. Mexican Cypress grows in a wide range of conditions, making it one of the most cultivated tree species in Mexico (CONAFOR 2017). In addition, because of the beauty of its foliage, it is planted in parks and gardens (Vazquez et al. 1999) and therefore constitutes one of the main components of the urban forest. This conifer is very susceptible to contamination and dehydration, which weakens the trees and favors the colonization of *P. tacubayae*. In some localities in central Mexico, the joint attack of this species along with *P. baumanni* Hopkins, 1905 occurs (CONAFOR 2017; Cibrián-Tovar et al. 2000). Although *P. tacubayae* is an important forest pest in the Mexican Official Norm (Cibrián-Tovar et al. 2000; SEMARNAT 2017), knowledge about its geographic range is based on old and biased sporadic collecting events in urban areas. In addition, its trophic spectrum has not yet been evaluated, and its current distribution is unknown.

Therefore, by combining revised previous collection records along with a new collection assembled by us, we evaluate the biotic (potential and actual hosts) and abiotic (temperature, precipitation, and altitudinal) conditions associated with this beetle species. We update the distribution of *P. tacubayae* and, using potential distribution models following the distribution range of the insect's host, explore new areas to corroborate its geographical distribution in natural and urban environments.

Methods

Analysis of geographical records. The geographical records of *Phloeosinus tacubayae* were obtained from Atkinson (2022) and from specimen records deposited in 13 entomological collections: Colección de Insectos Universidad Autónoma de Nuevo León, Linares (UANL), Mexico; Comisión Forestal del Estado de Michoacán, Morelia (COFOM), Mexico; Colección Científica de Entomología Forestal, División de Ciencias Forestales, Universidad Autónoma Chapingo (UACH), Mexico; Colección Entomológica del Instituto de Fitosanidad, Colegio de Postgraduados en Ciencias Agrícolas, Campus Montecillo (CEAM), Mexico; Universidad Autónoma del Estado de México, Estado de México (UAEM), Mexico; Colección Nacional de Insectos, Instituto de Biología Universidad Nacional Autónoma de México (CNIN), Mexico; Colección Entomológica de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB), Mexico; Laboratorio de Análisis de Referencia en Sanidad Forestal de la Secretaria de Medio Ambiente y Recursos Naturales, Coyoacán; Colección Entomológica del Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias, Coyoacán (INIFAP), Mexico; Colección Nacional de Insectos Museo de Historia Natural de la Ciudad de México, Mexico City (CNMHN), Mexico; Smithsonian Institution, National Museum of Natural History (USNM), USA; Zoological Museum, Lund (ZMLU), Sweden; Institut Royal des Sciences Naturelles de Belgique (IRSNB), Belgium.

The dataset for each geographical record included locality, coordinates, host species, collection date, and taxonomist. Records of *P. tacubayae* obtained from *Cupressus lusitanica* were considered as *Hesperocyparis lusitanica* following the current taxonomy. Those records lacking proper geographical coordinates were georeferenced in Google Earth Pro v. 91.40.0 (2020). All records included were supported by means of the identification of at least two adult specimens in the locality, either male or female. We identified each beetle specimen using morphological attributes from the head, pronotum, abdomen, and sculpture of the elytral declivity as proposed by Wood (1982).

Distribution. To visualize the spatial distribution of *P. tacubayae*, its occurrence records from North and Central America were mapped using ArcMap v. 10. 8 (ESRI 2020) using the Lambert conformal conic projection and the WGS84 geodetic datum. The current distribution of the species was described using both the states of the Mexican Republic layer and the biogeographic provinces of Mexico as proposed by Morrone (2020) and Morrone et al. (2017, 2022). The latter was chosen because it combines climatic, geological, and biotic criteria (Morrone et al. 2017). All records included in this study support that this bark beetle colonizes *H. lusitanica* trees. Therefore, to evaluate potential areas of presence and potential disjunctions related to the presence of its host, a database of occurrence data for this conifer (both as *C. lusitanica* and *H. lusitanica*; Adams et al. 2009) was downloaded from the Global Biodiversity Information Facility website (GBIF 2019a, 2019b) and projected along with the beetle occurrence data. To obtain the altitudinal range of both the beetle and host species, the altitude of each geographical record was extracted using ArcMap (ESRI 2020) with the Worldclim altitudinal layer enabled (Fick and Hijmans 2017). The spatial distribution of both insect and host records, plus the altitudinal range, were used together as a basis to describe the geographic distribution of *P. tacubayae* and to recognize possible disjunctions or biases in sampling related to the physiographic or ecological nature of habitats within its range.

To find new suitable collection sites, as well as to corroborate the presence of *P. tacubayae*, and to better understand the biological (host), climatic (temperature and precipitation), and altitudinal conditions favorable for the survival of this species throughout its known range, a potential distribution model was developed. The spatial model was performed based on 24 records, as some records were near one another; thus, records that were less than 30 km away from each other were excluded to avoid biases in the modeling (Boria et al. 2014; Merow et al. 2014; Guevara et al. 2018). The 19 bioclimatic and altitudinal variables were downloaded from the WorldClim database (Fick and Hijmans 2017) with a resolution of 30′. Values of each variable were extracted from the occurrence points using ArcGIS. To evaluate the correlation among environmental variables, a Peterson's test was performed to avoid collinearity of environmental variables; all correlated variables above 0.8 supported by Peterson's test were removed, and the most ecologically relevant variables according to the distribution model were chosen (Guevara et al. 2018). The potential distribution model was constructed using the Maxent algorithm with the selected variables. This algorithm yields more reliable estimates with sparse data (Phillips et al. 2006). The model was parameterized with the cloglog output with 20% training data, linear and quadratic features, and with five replicates (Phillips et al. 2017). The model was evaluated using the Receiver Operating Characteristic (ROC) partial curve test (Peterson et al. 2008) with the ntbox package in R (Osorio-Olvera et al. 2020). In addition, its predictive capacity was analyzed considering the omission rate (E = 5%) (Warren and Seifert 2011). The variables that contributed to the model, the least correlated and most ecologically relevant were BIO 05 (maximum temperature of the warmest month), BIO 06 (minimum temperature of the coldest month), and BIO 14 (precipitation of the driest month).

For its description, the model was projected on the map of the biogeographic provinces of Mexico (Morrone et al. 2017, 2022). Based on this projection, to conduct field sampling, establish new records, and corroborate the presence of *P. tacubayae* in some locations, which are representative of its geographic distribution, sites with high environmental suitability were selected in the north, center, and south of its known distribution. The collection sites were selected in areas on the boundary and at the center of its distribution: in the north, in the state of Nuevo León; in the center, from Mexico and Michoacan states; and in Guatemala (Table 1).

Material collected. The specimens collected from localities with high suitability supported by the potential distribution maps were deposited in the CNIN, with their respective collection permits issued by Secretaría del Medio Ambiente y Recursos Naturales, Mexico (FAUT-0352, FAUT-0353).

Results

Historical and new records, as well as the collection sites selected by the potential distribution model, are listed below. Each type of record is indicated in Table 1. At four collection sites, *Phloeosinus tacubayae* was found colonizing *Hesperocyparis lusitanica* trees (Table 1). Infested trees showed characteristics produced by the activity of this bark beetle: yellow to red foliage color (Fig. 1A–C), inconspicuous resin runoff on the bark, and the presence of frass created by the colonizing bark beetles (Fig. 1D, E), which accumulates in the crevices of the trees, resembling a very finely ground, cream-brown material on the bark. In the phloem, the gallery systems were observed (Fig. 1E), consisting of a longitudinal parental tunnel and transverse larval tunnels around the parental tunnel (Fig. 1F, G).

Materials examined. MEXICO – **Ciudad de México** • Chapultepec; 19°24′58″N, 099°11′53″W; VI/1962; R.H. Bernal leg.; host: *Cupressus* sp.; 2 sex indet., UACC; 3862 • Miguel Hidalgo, ENCB; 19°45′04″N, 099°16′08″W ; 14/IV/2009; FAT leg.; *H. lusitanica*; 2 sex indet., CNIN-M07 • Cd. Universitaria; 19°19′20″N, 099°11′08″W; 11/VIII/1983; SA Burgos leg.; host: *Cupressus* sp.; 4 sex indet., CNIN-B056 • Tlalpan; 19°17′00″N, 099°10′00″W; 16/IX/1949; J.P. Perry leg.; host: *H. lusitanica* as *Cupressus lindleyi*; 2 sex indet., CNIN-M07 • Iztapalapa; 19°26′04″N, 099°08′18″W; 24/VI/1905; host: *Cupressus* sp.; 2 sex indet., CNIN-2728 • Magdalena Contreras; 19°20′07″N, 099°12′49″W; host: *H. lusitanica*; 2 sex indet., CNIN-41 • Cuauhtémoc, Alameda central; 19°23′03′N′, 099°08′38″W; 06/V/2014; host: *H. lusitanica*; 4 sex indet., CNIN-M08 – **Estado de México** • Tecámac, Boulevard Hacienda Ojo de Agua; 19°40′11″N, 099°01′5″W; 15/VI/19; FAT leg.; host: *H. lusitanica*; 4 sex indet., CNIN-M04 • Iztaccíhuatl, Cañada el paraje; 19°05′14″N, 98°40′03″W; 14/10/19; M. Cervantes, FAT leg.; host: *H. lusitanica*; 5♂, 5♀, CNIN-M02 • Texcoco; 19°30′20″N, 098°52′55″W; 16/VI/1979; T.H. Atkinson. leg.; host: *H. lusitanica* as *C. lindleyi*; 5 sex indet., CNIN-180 • Amecameca; 19°07′40″N, 098°45′46″W; 9/VI/1982; M.A. Equihua leg.; *H. lusitanica* as *C. lindleyi*; 3 sex indet., CNIN-S714 • San José del Rincón; 19°39′51″N, 100°09′52″W; 09/XI/2016; J.L. Escobar-Betanzos leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M30 • San Martín de las Pirámides;

19°37′45″N, 098°44′46″W; 27/VIII/2018; G. Natividad-Martínez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M31 • Otumba, Jaltepec; 19°39′01″N, 098°41′19W; 11/XI/2019; G. Natividad-Martínez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M32 • Otumba, Las Palomas; 19°39′01″N, 098°41′19″W; 12/II/2020; G. Natividad-Martínez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M33 • Acambay, Agua Limpia; 19°42′48″N, 099°58′4″W; 11/III/2020; J.L. Escobar-Betanzos leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M34 • Temascalcingo, Bordo de las Guajolotas; 19°54′55″N, 099°49′18″W; 02/X/2020; J.L. Escobar-Betanzos leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M35 • Chiautla, Xentlapa, San Lucas Huitzilhuacan; 19°55′N, 100°07′W; 16/III/2021; S. Nava-

Table 1. Records of *Phloeosinus tacubayae* in Mexico, Guatemala, El Salvador, Nicaragua. [a] historical record, [b] new record.

Country	State	Locality	Latitude (N)	Longitude (W)	Altitude a.s.l. (m)	Host	Date collected	Collection*/ voucher
Mexico								
a	Ciudad de México	Magdalena Contreras	19°20′7.3″	099°12′49.2″	2355	*Hesperocyparis lusitanica*	—	CNIN-41
a	Ciudad de México	Cuauhtémoc, Alameda central	19°23′03″	099°08′38″	2239	*Hesperocyparis lusitanica*	06/V/2014	CNIN-M08
a	Ciudad de México	Tlalpan	19°17′00″	099°10′00″	2304	*Hesperocyparis lusitanica*	16/IX/1949	CNIN-M07
a	Ciudad de México	Universidad Nacional Autónoma de México	19°19′20″	099°11′08″	2292	*Cupressus* sp.	11/VIII/1983	CNIN-B056
	Ciudad de México	Chapultepec	19°24′58″	099°11′53″	2581	*Cupressus* sp.	VI/1962	UACC 3862
	Ciudad de México	Iztapalapa	19°26′04″	099°08′18″	2243	*Hesperocyparis lusitanica*	24/VI/1905	CNIN-2728
a	Ciudad de México	Miguel Hidalgo, ENCB	19°45′04″	099°16′08″	2273	*Hesperocyparis lusitanica*	14/IV/2009	CNIN-M07
b	Estado de México	Tecámac, Boulevard Hacienda Ojo de Agua	19°40′11′′	099°01′05″	2328	*Hesperocyparis lusitanica*	15/VI/19	CNIN-M04
b	Estado de México	Cañada el paraje	19°05′14″	098°40′03″	3201	*Hesperocyparis lusitanica*	14/10/2019	CNIN-M02
a	Estado de México	Amecameca	19°07′40″	098°45′46″	2447	*Hesperocyparis lusitanica*	9/VI/1982	CNIN-S714
a	Estado de México	San José del Rincón	19°37′45″	098°44′46″	2535	*Hesperocyparis lusitanica*	09/XI/2016	CNIN-M30
a	Estado de México	San Martín de las Pirámides	19°39′01″	098°41′19″	2609	*Hesperocyparis lusitanica*	27/VIII/2018	CNIN-M31
a	Estado de México	Otumba	19°39′01″	098°41′19″	2828	*Hesperocyparis lusitanica*	11/XI/2019	CNIN-M32
a	Estado de México	Otumba	19°42′48″	099°58′04″	2699	*Hesperocyparis lusitanica*	12/II/2020	CNIN-M33
a	Estado de México	Acambay	19°54′55″	099°49′18″	2398	*Hesperocyparis lusitanica*	11/III/2020	CNIN-M34
a	Estado de México	Temascalcingo	19°55′00″	100°07′01″	2352	*Hesperocyparis lusitanica*	02/X/2020	CNIN-M35
a	Estado de México	Chiautla	19°47′07″	099°34′56″	2379	*Hesperocyparis lusitanica*	16/III/2021	CNIN-M36
a	Estado de México	Temamatla	19°35′03″	098°52′32″	2425	*Hesperocyparis lusitanica*	13/IV/2021	CNIN-M38
a	Estado de México	Coacalco de Berriozábal	19°11′09″	098°51′42″	2534	*Hesperocyparis lusitanica*	14/VI/2021	CNIN-M39
a	Estado de México	Apaxco de Ocampo	19°36′41″	099°07′06″	2450	*Hesperocyparis lusitanica*	09/VII/2021	CNIN-M40
a	Estado de México	La Paz	19°53′50″	099°11′21″	2446	*Hesperocyparis lusitanica*	14/VII/2021	CNIN-M41
a	Estado de México	Hueypoxtla	19°59′19″	099°03′38″	2636	*Hesperocyparis lusitanica*	28/VII/2021	CNIN-M42
a	Estado de México	San Felipe del Progreso	19°18′25″	099°41′28″	2518	*Hesperocyparis lusitanica*	19/VII/2021	CNIN-M43
a	Estado de México	Chapa de Mota	19°37′04″	099°54′59″	2716	*Hesperocyparis lusitanica*	22/VI/2021	CNIN-44
a	Estado de México	Toluca	19°37′04″	099°54′59″	2716	*Hesperocyparis lusitanica*	18/VIII/2020	CNIN-45
a	Estado de México	Texcoco	19°30′20″	098°52′55″	2256	*Hesperocyparis lusitanica*	16/VI/1979	CNIN-180
a	Hidalgo	Epazoyucan, Tuzoofari	20°01′19″	098°38′54″	2100	*Hesperocyparis lusitanica*	20/VII/2018	CNIN-M29
a	Hidalgo	Tulancingo	20°08′00″	098°08′59″	2134	*Hesperocyparis lusitanica*	10/VII/1967	USNM SLW-17
a	Michoacán	Quiroga, Santa Fe de la laguna, paraje Chapil y Cumur	19°40′29″	099°01′05′	2067	*Hesperocyparis lusitanica*	23/X/2021	CNIN-M20
a	Michoacán	Uruapan	19°25′34″	102°03′41″	1663	*Hesperocyparis lusitanica*	19/II/1980	CNIN-S033
b	Monterrey, Nuevo León	Galeana, Jardín particular cerca de cab. Municipal	24°49′21″	100°05′04″	1686	*Hesperocyparis lusitanica*	—	CNIN-M01
b	Monterrey, Nuevo León	Iturbide	24°49′20.5″	100°05′03.6″	1132	*Hesperocyparis arizonica*	11/III/1982	CNIN-276
a	Morelos	Cuernavaca	18°55′07″	099°14′03″	1536	*Cupressus* sp.	25/IX/1982	CNIN-SM021
a	Morelos	Huitzilac	19°01′42″	099°16′02″	2559	*Hesperocyparis lusitanica*	6/IX/1981	CNIN-M06
a	Morelos	Tres Marias	19°03′15″	099°14′30″	2823	—	15/V/1982;	CNIN-S650
a	Tlaxcala	Temetzontla	19°21′09″	098°17′15″	2569	trap: Lindgren	—	CNIN-M05
a	Veracruz	Naolinco	19°39′12″	096°52′25″	1554	*Cupressus* sp.	28/I/1984	CNIN-FANM-119
Nicaragua								
b	Esteli	La Almaciguera	12°59′28″	086°21′55″	1404	*Hesperocyparis lusitanica*	14/III/2010	CNIN-THA924
El Salvador								
a	El Salvador		13°40′12″	088°51′43″	713	—	—	unknown
b	Ahuachapan	Apaneca	13°51′35″	089°48′12″	1453	*Hesperocyparis lusitanica*	14/VII/1959	IRSNB-126096
Guatemala								
b	Chimaltenango	El tejer	14°37′39″	090°47′11″		*Hesperocyparis lusitanica*	05/IV/2018	CNIN-M03
a	Escuintla	Volcan el agua	14°28′26″	090°42′43″	2199	*Hesperocyparis lusitanica*	19/V/1964	USNM-SLW-597
a	Sacatepequez	San Miguel Dueñas	14°31′25″	090°48′58″	1503	*Cupressus* sp.	11/IX/1977	CNIN-180
	Sololá	Panajachel	14°55′59″	091°37′59″	2651	—	11/XI/1991	ZMLU

* The acronyms of insect collections are presented in Methods.

Figure 1. Habitat of *Phloeosinus tacubayae*. **A.** *Hesperocyparis lusitanica* plantation in Michoacán, Mexico. **B.** Close-up of trees attacked by the bark beetle. **C.** Tree with active outbreak knocked down. **D.** Frass on host bark. **E.** Tree debarked to expose the phloem and gallery systems. **F.** Gallery system. **G**. Male and female within the parental gallery. The white arrows point out trees with active beetle outbreaks (A), entry holes surrounded by frass (B), and eggs in a parental tunnel. Abbreviations: LT, larval tunnels; NC, nuptial chamber; PC pupal chamber; PT, parental tunnel.

Gómez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M36 • Temamatla, Campo Militar Temamatla 37B; 19°35′3″N, 099°34′56″W; 13/IV/2021; P. Morales-Ramón leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M38 • Coacalco de Berriozabal, Sierra gorda, La Presa, Aguilillas; 19°35′03″N, 098°52′32″W; 14/VI/2021; R. Maciel-Figueroa leg.; host: *Hesperocyparis lusitanica*; 2 sex indet., CNIN-M39 • Apaxco de Ocampo, Apasca, Las mesas; 19°11′9″N, 98°51′42″W; 09/VII/2021; R. Maciel-Figueroa leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M40 • San Sebastián Chimalpa, La Paz, El Cedral; 19°36′41″N, 099°07′06″W; 14/VII/2021; S. Nava-Gómez leg.; host: *Hesperocyparis lusitanica*; 2 sex indet., CNIN-M41 • Hueypoxtla, Ajuloapan; 19°53′50″N, 099°11′21″W; 28/VII/2021; S. Nava-Gómez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M42 • San Felipe del Progreso, San Pedro el Chico; 19°59′19″N,

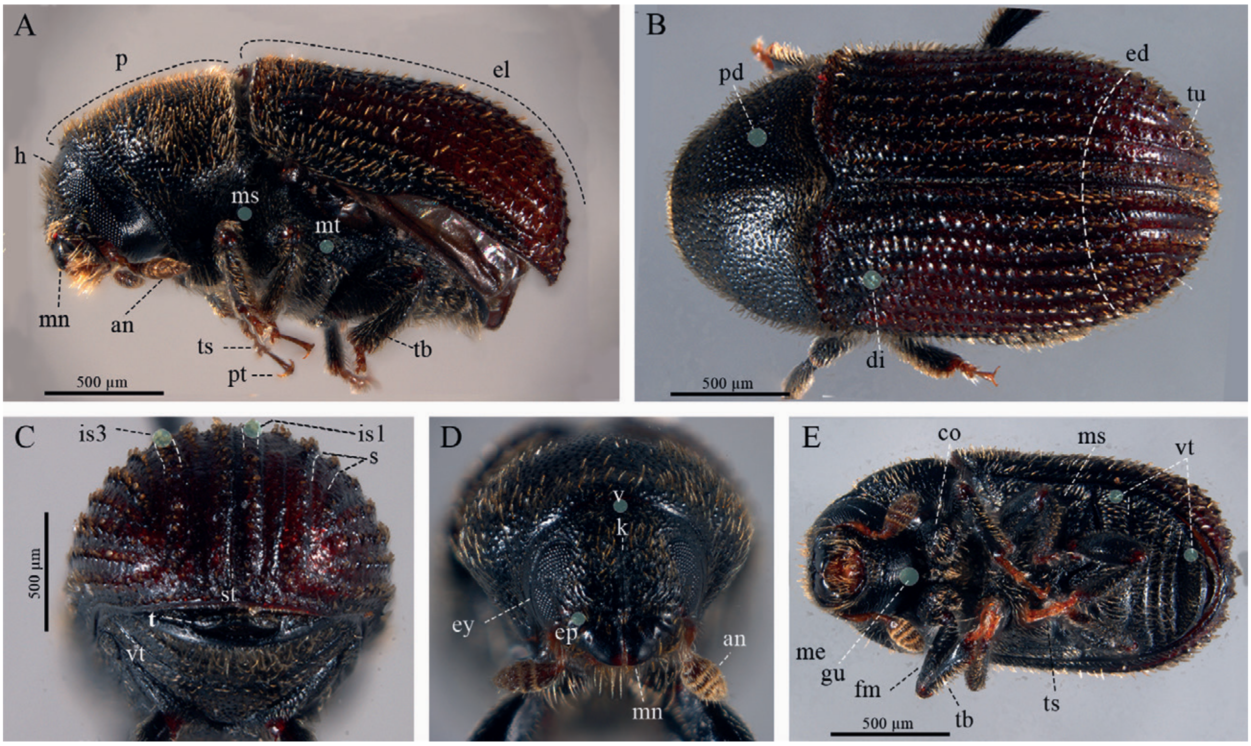

Figure 2. Adult male of *Phloeosinus tacubayae*. **A.** Lateral view. **B.** Dorsal view. **C.** Elytral declivity. **D.** Head. **E.** Ventral view. Abbreviations: an, antenna; co, coxa; di, disc; ed, elytral declivity; el, elytra; ey, eye; fm, femur; gu, gula; h, head; is1, interstriae one; is3, interstriae three; k, keel, me, mentum; mn, mandible; ms, mesothorax; mt, metathorax; p, pronotum; pd, pronotal disc; pt, pretarsus; s, striae; st, suture; t, tergite; tb, tibia; ts, tarsus; tu, tubercle; v, vertex; vt ventrites.

099°03′38″W; 19/VII/2021; J.L. Escobar-Betanzos leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M43 • Chapa de Mota, Cenqui, La loma; 19°47′50″N, 099°35′20″W; 22/VI/2021; J.L. Escobar-Betanzos leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M44 • Toluca, Sierra de Morelos; 19°37′04″N, 099°54′59″W; 18/VIII/2020; M. De-Luna-Martínez leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M45 – **Hidalgo** • Tulancingo, 35 km E; 20°08′00″N, 098°08′59″W; 10/VII/1967; S.L. Wood leg.; host: *H. lusitanica*; 1 sex indet., USNM; SLW-17 • Epazoyucan, Tuzoofari; 20°01′19″N, 098°38′54″W; FAT & MCE leg.; host: *Hesperocyparis lusitanica*; 6 sex indet., CNIN-M29 – **Michoacán** • Quiroga, Santa Fe de la laguna, paraje Chapil y Cumur; 19°40′29″N, 101°31′38″W; 23/X/21; FAT & MCE leg.; host: *H. lusitanica*; 5♀, 5♂, CNIN-M20 • Uruapan; 19°25′34″N, 102°03′41″W; 19/II/1980; T.H. Atkinson leg.; host: *H. lusitanica* as *C. lindleyi*; 5 sex indet., CNIN-S033. – **Morelos** • Cuernavaca; 18°55′07′′N, 099°14′03″W; 25/IX/1982; S.A. Burgos & C.E. Saucedo leg.; host: *Cupressus* sp.; 1 sex indet., CNIN-SM021• Tres Marías; 19°03′15″N, 099°14′30″W; 15/V/1982; S.A. Burgos & C.E. Saucedo leg.; 6 sex indet., CNIN-S650 • Huitzilac; 19°01′42″N, 099°16′02″W; 6/IX/1981; S.A. Burgos leg.; host: *H. lusitanica* as *C. lindleyi*; 5 sex indet., CNIN-M06 – **Nuevo León** • Iturbide, Ejido la Purisima; 24°32′32′N″, 099°49′30″W; 11/III/1982; L.J. Flores leg.; host: *H. arizonica*; 3 sex indet., CNIN-276 • Galeana, Jardín particular cerca de cab. Municipal; 24°49′21″N, 100°05′04″W; 22/XI/2018; M. Cervantes, FAT leg.; host: *H. lusitanica*; 5♀, 5♂, CNIN-M01 – **Tlaxcala** • Temetzontla; 19°21′09″N, 098°17′15″W; trap: Lindgren funnel; 1 sex indet., CNIN-M05 – **Veracruz** • Naolinco; 19°39′12″N, 096°52′25″W; 28/I/1984; M. Noguera & FAT leg.; host: *Cupressus* sp.; 8 sex indet., CNIN-FANM-119.

GUATEMALA – **Chimaltenango** • El Tejer; 14°37′39″N, 090°47′11′′W; 05/IV/2018; JFGO leg.; host: *H. lusitanica*; 2 sex indet., CNIN-M03 – **Escuintla** • Volcán del agua; 14°28′26″N, 090°42′43″W; 19/V/1964; S.L. Wood leg.; host: *H. lusitanica*; 1 sex indet., USNM-SLW-597 – **Sacatepequez** • San Miguel Dueñas; 14°31′25″N, 090°48′58″W; 11/IX/1977; R. López leg.; host: *Cupressus* sp.; 5 sex indet., CNIN-180. **Sololá** • Panajachel; 14°55′59″N, 091°37′59″W; 11/XI/1991; R.M. Baranowski leg.; with punching net; 1 sex indet., ZMLU

EL SALVADOR – **Ahuachapan** • Apaneca; 13°51′35″N, 089°48′12″W; 14/VII/1959; Bechyné, J. leg.; 1 sex indet., IRSNB-126096 • El Salvador; 13°40′12″N, 088°51′43″W; T.H. Atkinson leg.1 sex indet.

NICARAGUA – **Estelí** • La Almaciguera; 12°59′28″N, 086°21′55″W; 14/III/2010; T.H. Atkinson leg.; host: *H. lusitanica*; 20 sex indet., CNIN-THA924.

Identification. All examined adults displayed the morphological characters proposed for the identification of *P. tacubayae* (Hopkins 1905; Wood 1982). Males and females 1.8–2.4 mm long, dark reddish, with pubescence over entire body surface and scale-like seta on elytral declivity (Fig. 2A–E); head short, with convex frons; eyes elongate and conspicuously emarginated; antennal club asymmetrically compressed, with tree aseptate

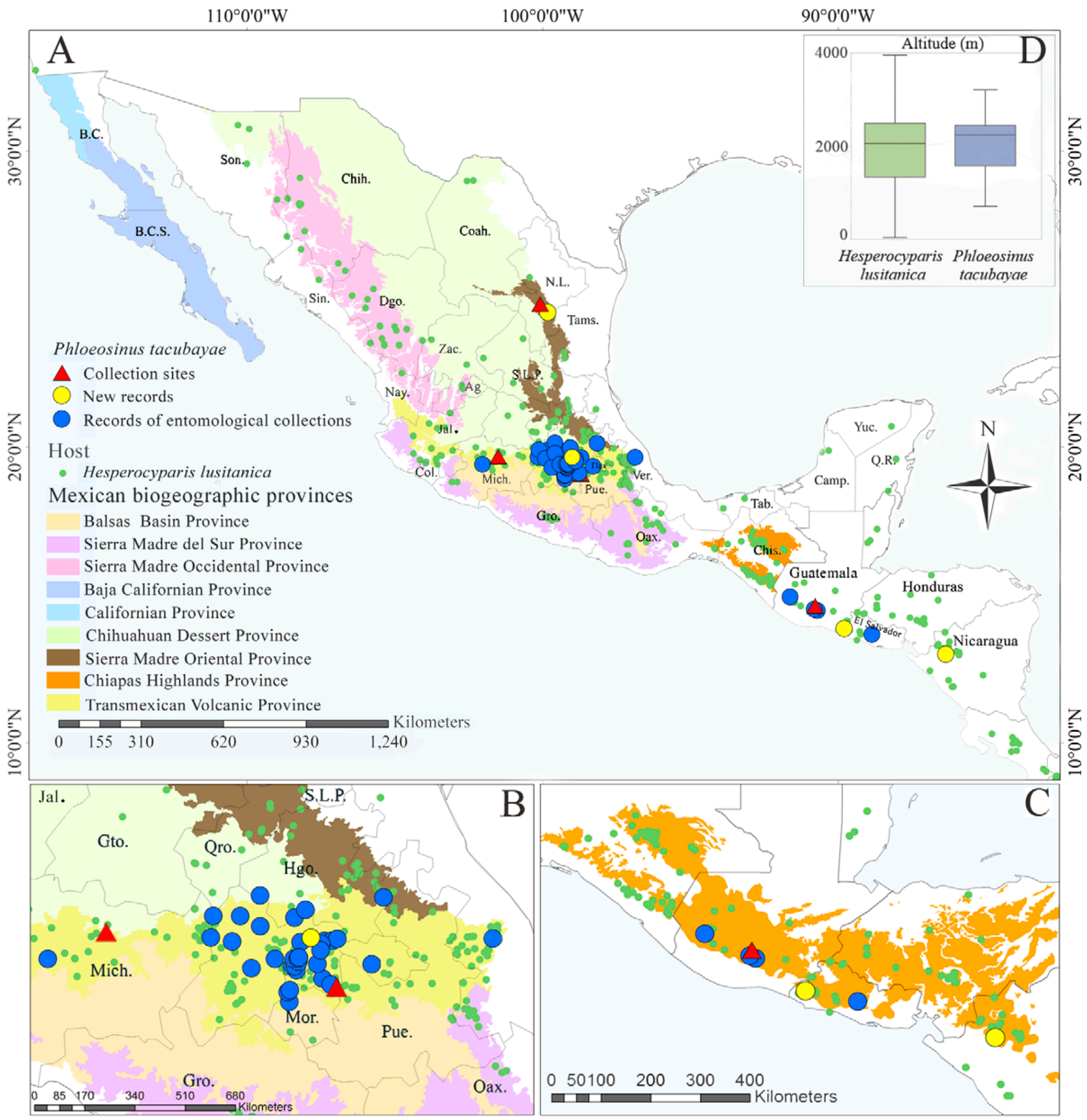

Figure 3. Geographical distribution of *Phloeosinus tacubayae* in Mexico and Central America, **A.** Distribution of *Phloeosinus tacubayae* and its host *Hesperocyparis lusitanica* using the biogeographical provinces of Mexico. **B**. Distribution of the beetle and its host in the Transmexican Volcanic belt Province. **C**. Distribution of the beetle and its host in the Chiapas Highlands Province. **D.** The altitudinal ranges of the host and the beetle, the altitudinal of the beetle is within the host. Abbreviations: Ag. Aguascalientes; B. C., Baja California Norte; B. C. S., Baja California Sur; Camp., Campeche; Chih., Chihuahua; Chis., Chiapas; Coah., Coahuila; Col., Colima; Dgo., Durango; Jal., Jalisco; Mich., Michoacán; Nay., Nayarit; N. L., Nuevo León; Oax., Oaxaca; Pue., Puebla; Q. R., Quintana Roo; S. L. P., San Luis Potosí; Sin., Sinaloa; Son., Sonora; Tab., Tabasco; Tams., Tamaulipas; Tlax., Tlaxcala; Ver., Veracruz; Yuc., Yucatán; Zac., Zacatecas.

sutures, with a sharply elevated medial carina from epistomal margin to upper level of eyes (Fig. 2A, D, E); pronotum disc with small, deep, close punctures and stout, short, abundant pubescence; entire elytral disc with yellow pubescence, punctures, and less abundant scale-like seta on declivity (Fig. 2A, B); elytral slope convex (Fig. 2B, C); interstriae wider than striae; first and third interstriae with small, rounded, serial tubercles (Fig. 2B); first interstriae with three large tubercles and the other ones narrower, with abundant setae and scale-like seta (Fig. 2C).

Geographical distribution. Forty-four occurrence records of *P. tacubayae* were found (Table 1, Fig. 3A) in insect collections and corroborated by morphological identifications. Of these records, 70% are from the Transmexican Volcanic Belt (TVP) (Table 1, Fig. 3B) biogeographic province, and 30% are from the Sierra Madre Oriental Province (SMORP) and the Chiapas Highlands Province (CHP) in southern Mexico, Guatemala, Honduras, El Salvador, and Nicaragua (Fig. 3C). All records are from areas where the host species, *H. lusitanica*, occurs. Furthermore, *P. tacubayae* is distributed in an altitudinal range of 713–3210 m a.s.l. (mean: 2089 m), while the altitudinal range of its main host is 3–3955 m a.s.l. (mean: 1901 m), suggesting that this insect has a narrower altitudinal range than its host (Fig. 3D).

The potential distribution map shows four regions with the highest probability of finding the species in the

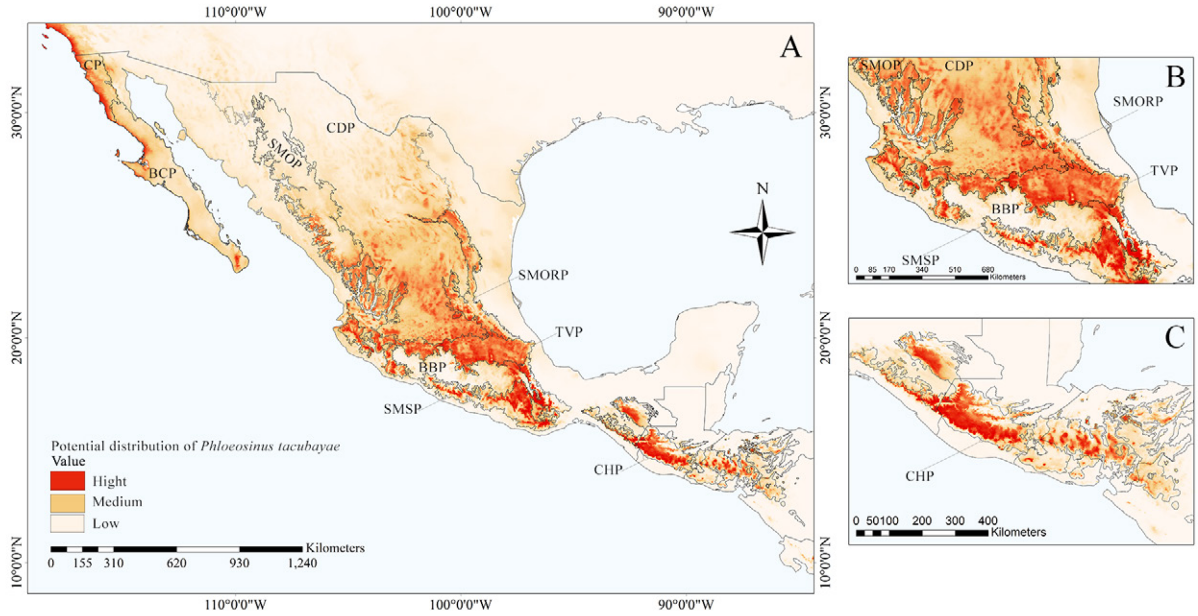

Figure 4. A. Potential distribution of *Phloeosinus tacubayae*. **B.** Potential distribution in the Transmexican Volcanic belt Province. **C.** Potential distribution in the Chiapas Highlands Province. Abbreviations: BCP, Baja Californian Province; BBP, Balsas Basin Province; SMSP, Sierra Madre del Sur Province; CP, Californian Province; CHP, Chiapas Highlands Province; CDP, Chihuahuan Desert Province; SMOP, Sierra Madre Occidental Province; SMORP, Sierra Madre Oriental province; TVP, The Transmexican Volcanic Belth Province.

SMORP, the TVP, the Sierra Madre del Sur Province (SMSP), and the CHP, (Fig. 4A). There were also very small and scattered areas with medium suitability in the Baja California Province (BCP), the California Province (CP), the Sierra Madre Occidental Province (SMOP), the Chihuahuan Desert Province (DCP), and the Balsas Basin Province (BBP). In the SMORP, southeast Coahuila, central Nuevo León, and western Tamaulipas are areas of high environmental suitability that favors the presence of *P. tacubayae* (Fig 4B). In the TVP the most extensive and continuous regions with a high probability of finding the species are in the east of the province in Mexico state, Hidalgo, Tlaxcala, Puebla, Morelos, and Guerrero, and southeastern Puebla, and western Veracruz; smaller discontinuous areas are also in the central to southern portions of Jalisco, Michoacán, and Mexico state, and the central to northern portions of Jalisco, Guanajuato, Querétaro, Hidalgo, Michoacán, and Mexico state (Fig. 4B). In the SMSP, the entire province shows a high probability of finding the species; in the eastern portion of the province the highest probability is found in Michoacán and Guerrero, and in the Oaxacan Highlands; in the westernmost portion of the SMSP, there are small and discontinuous zones in Jalisco (Fig. 4B). In the CHP, the probability of finding the species is also high, in western Oaxaca, eastern Chiapas and Oaxaca, northern Chiapas, the lowlands of Chiapas and Guatemala, and the highlands of Guatemala and Nicaragua, where there is an extensive discontinuous area of high suitability (Fig. 4C).

Habitats. Most of the specimens were found colonizing *H. lusitanica*. Only one record in the state of Nuevo Leon presented *H. arizonica* as the host. The records were obtained mostly from urban areas in trees older than 10 years and with considerable density. In Uruapan, Michoacán, *P. tacubayae* was found in a pine forest in a cultivate area *H. lusitanica* trees between 10 and over 20 years old. In Iztaccíhuatl, Mexico state, *P. tacubayae* was found in a fir–cypress mountain forest in a more than 80-year-old, felled *H. lusitanica* tree. In Nuevo León, *P. tacubayae* was found coexisting with *P. serratus* Le Conte, 1868 in the same host and part of the tree, while in Iztaccíhuatl, *P. tacubayae* was found coexisting with *P. baumanni*.

Discussion

Phloeosinus tacubayae was described in 1905 from a single locality in Tacubaya, Mexico City (Hopkins 1905). Since then, several authors have provided new records in the Valley of Mexico, around the type locality, and in other Mexican states and Central American countries (Blackman 1942; Wood 1982; Atkinson and Equihua 1985; Bright and Skidmore 1997; Atkinson 2022). Previous occurrence records, together with our new records, support that the distribution of *P. tacubayae* extends to at least eight states (Mexico City, Estado de México, Hidalgo, Tlaxcala, Veracruz, Morelos, Michoacán, Nuevo León) and to three Central American countries (Guatemala, Nicaragua, and El Salvador); potentially it may occur in Baja California Norte, Baja California Sur, Nayarit, Coahuila, Durango, Zacatecas, San Luis Potosi, Aguascalientes, Tamaulipas, Colima, Jalisco, Guanajuato, Queretaro, Puebla, and Chiapas states.

The distribution pattern of *P. tacubayae* belongs to the Nearctic cenocron, which corresponds to North American taxa that dispersed southward during the Miocene and Pleistocene to the biogeographic provinces of

SMOP, SMORP, SMSP, CVTP, and CHP (Halffter 1964, 1987, 2017; Halffter and Morrone 2017; Escalante et al. 2021; Morrone 2020). The species is mainly distributed in mountainous areas, in mesophyll mountain forests, temperate forests, and coniferous forests. Our results support that *P. tacubayae* is an oligophagous species that colonizes *H. lusitanica* and *H. arizonica*, but with most records from the first species. Like other oligophagous Scolytinae species (e.g., *Dendroctonus pseudotsugae pseudotsugae* Hopkins, 1909 and *Dendroctonus ponderosae* (Hopkins, 1902)) (Huber et al. 2009), the distribution of *P. tacubayae* is strongly conditional on its host (Ruiz et al. 2009; Mendoza et al. 2011). According to the biogeographical history of *Hesperocyparis*, both host species of *P. tacubayae* are included in the Arizonica clade (Terry et al. 2012), which migrated from northern to southeastern North America during the mid-Miocene, colonizing arid and mountain zones from northern Mexico to Central America (Terry et al. 2016); *Hesperocyparis* species are also Nearctic cenocrons.

The potential distribution models of bark beetles from Mexico and Central America have mainly focused on the evaluation of the probability of colonizing new areas, and the risk derived from climate change allowing them to access new environments soon (Evangelista et al. 2011; González-Hernández et al. 2020). Therefore, the models almost always describe their distribution artificially, focusing on the predictive capacity of the models. Few studies focus on the spatial distribution of bark beetle species by considering the presence of their known hosts in ecologically relevant areas and examining whether hosts really limit the geographic distribution of the beetles (e.g., Salinas-Moreno et al. 2010; Mendoza et al. 2011; Armendariz-Toledano et al. 2017). Our potential distribution model supports the existence of favorable environmental conditions for the establishment of *P. tacubayae*, in both previously known and new areas where its host is present. The bioclimatic variables were the most important in the model (maximum temperature of the warmest month, minimum temperature of the coldest month, and precipitation of the driest month), which are closely related to the optimal conditions that *H. lusitanica* needs to survive (CONAFOR 2017). Despite the altitude in some cases significantly increasing the accuracy of predicted species distribution ranges (Hof et al. 2022), in our study, this variable was not considered, because it did not have a significant effect on the predictive power of models and correlated with bioclimatic variables. This shows that the distribution of *P. tacubayae* is closely associated with its host, which is considered an endemic species of Mesoamerica in Mexico and Central American countries (CONAFOR 2017). This indicates that the host must be considered as a delimiting factor in the distribution *P. tacubayae* and considered as necessary for its dispersal (Barve et al. 2011). Although *P. tacubayae* was also recorded in *Hesperocyparis arizonica*, the natural distribution of this species is restricted to the southern United States and northern Mexico, so more sampling is required to contemplate and corroborate it as another host, since these species overlap their latitudinal and longitudinal distribution range considerably with *H. lusitanica* and both are closely phylogenetically related (Terry et al. 2016).

In the four collection sites selected from the potential distribution model, the presence of *P. tacubayae* was supported, confirming the predictive power of distribution models. We note that the model also showed favorable conditions in regions that were not corroborated by new sampling, such as the Chihuahuan Desert Province, the California Province, and the Baja California Province. These areas have the potential to support the presence of the insect, as its host is a popular species in Mexico as an ornamental tree (CONAFOR 2017) and populations can be found in patches in urban forests or ornamental trees in these areas. A future objective is to sample these areas.

The colonization pattern of *P. tacubayae* resembles that of other species such as *P. rudis* Blandford, 1894 (Mendel 1984; Moraal 2010) and *P. aubei* Perris, 1855 (Fiala and Holuša 2019). The coloration of the trees always changes to reddish, and the galleries consist of a central parental tunnel in which the female lays eggs neatly on both sides, as indicated by Mendel (1984) and Cibrián-Tovar et al. (2000). Our results support that this beetle is widespread throughout urban areas and plantations in natural areas, especially where its host trees are in high densities. Under stress conditions, this insect can develop massive attacks, weakening the defenses of the trees, and causing the death of dozens of trees. However, in natural areas, it colonizes fallen trunks or felled trees (early saprophytic).

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Authors' Contributions

Conceptualization: MCE, FAT. Data curation: MCE, FAT, THA, JFGO. Formal analysis: MCE, FAT. Funding acquisition: EAR, GCR. Methodology: MCE, FAT, JFGO. Project administration: GCR, FAT. Resources: MCE, FAT, THA, GCR, EAR. Software: MCE. Supervision: FAT, GCR, THA. Validation: FAT, THA, EAR. Visualization: MCE, FAT. Writing – original draft: MCE, FAT. Writing – review and editing: MCE, FAT, GCR, THA, EAR. Research: MCE, FAT, THA, EAR.

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