Research Article

Received: 1 February 2019 Revised: 12 October 2019 Accepted article published: 28 October 2019 Published online in Wiley Online Library: 27 November 2019

(wileyonlinelibrary.com) DOI 10.1002/ps.5663

Inter-country trade, genetic diversity and bio-ecological parameters upgrade pest risk maps for the coconut hispid *Brontispa longissima*

Baoqian Lu,[a] Zhengqiang Peng,[a] Hui Lu,[a] Fan Yang,[b] Peiqun Lin,[a] Xiaoqiang Chu,[a] Xing He[a] and Jihong Tang[a*]

Abstract

BACKGROUND: Invasions of a number of tree-feeding beetles have increased globally and pose a mounting threat to the world's trees, production forests and natural habitats. An in-depth understanding of the determinants of invasion potential of a given species and invasibility of novel environments can help forecast future invasions and avert undesirable socio-economic impacts. Here, we quantitatively assess the (multivariate) drivers of historic invasions of the coconut hispid *Brontispa longissima* (Coleoptera: Chrysomelidae) across the Asia-Pacific region and critically assess its invasion potential for other key coconut-growing regions.

RESULTS: Genetic variation of *B. longissima* in its invaded range indicated multiple incursions, likely associated with (short-range) natural dispersal and (long-range) trade in ornamental palms and coconut plantlets. Interception records at China's ports of entry accentuate the role of traded planting material. The high fecundity and prolonged, yet adaptable, oviposition period of *B. longissima* further enhance the invasiveness of this species and aid its successful establishment. Coconut-growing areas are identified with high climatic suitability for *B. longissima*, and where strengthened biosecurity protocols can prevent future invasions.

CONCLUSION: A combined assessment of inter-country trade patterns, population genetics and species bio-ecology (e.g. climate-related development) illuminates the dispersal pathways of invasive species, assesses invasibility of particular geographies, guides quarantine interventions and thus can effectively avert future invasions.

Supporting information may be found in the online version of this article.

Keywords: invasive beetles; *Brontispa longissima*; global trade; biological trait; invasion biology

1 INTRODUCTION

In recent years, the incidence, population pressure and pest status of myriad tree-feeding beetles has increased globally and poses a non-negligible threat to forestry and natural environments in both temperate and tropical settings.[1–4] Comprising a diverse set of taxa within the order Coleoptera (e.g. Buprestidae, Cerambycidae, Chrysomelidae, Curculionidae and Scarabaeidae), these organisms consume leaves, affect bark or bore into the trunks, roots or branches of woody plants. Invasive species such as *Rhynchophorus ferrugineus* Olivier, *Anoplophora glabripennis* Motchulsky or *Agrilus planipennis* Fairmaire are decimating ornamental trees, natural forests and fruit-bearing palms in different parts of the world.

The coconut leaf beetle *Brontispa longissima* (Gestro) feeds on young leaves and seedlings of the coconut palm, *Cocos nucifera* L. Over the past decades, *B. longissima* has spread across the Asia-Pacific region and is causing considerable environmental and socio-economic impacts, especially in areas where coconut cultivation sustains rural livelihoods.[5,6] Native to Indonesia and/or Papua New Guinea, *B. longissima* made its initial incursions into several Pacific Islands in the early 20th century and subsequently invaded Vietnam, Cambodia, Laos, Thailand, Maldives, Myanmar, China and the Philippines.[6] In invaded areas, *B. longissima* rapidly reaches 70–90% incidence in both managed and natural coconut stands, inflicting production losses as high as 50–70%.[7] In 1999, *B. longissima* was detected in China's Guangzhou province, and its subsequent spread across southern parts of the country and

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* *Correspondence to: J Tang, Environment and Plant Protection Institute, Chinese Academy of Tropical Agricultural Sciences, Haikou 571 101, Hainan Province, China. E-mail: jihong_23@163.com*

a *Key Laboratory of Integrated Pest Management on Tropical Crops, Environment and Plant Protection Institute, Chinese Academy of Tropical Agricultural Sciences, Haikou, China*

b *College of Forestry, Hainan University, Haikou, China*

neighboring Asian nations is thought to be primarily anthropogenic, i.e. through trading of palm plants.

Species can become invasive once they arrive in environments to which they are not native, and then successfully establish, spread and inflict harm on resident organisms.[8,9] Although no universal suite of features or 'traits' can reliable predict a species' invasiveness, various traits are associated with the invasion potential of particular taxa (and specific habitats). For exotic fish, species with rapid growth rates and wide tolerance of temperature and salinity are more likely to become established following their introduction.[10] Other traits that favor a species' invasiveness are a short generation time, phenotypic plasticity, high reproductive capacity and cold-hardiness.[11–13] The ability of certain organisms, e.g. tree-feeding beetles, such as *B. longissimi*, to colonize new environments is also further enhanced by their association with internationally traded ornamental plants, live seedlings or wood, e.g. packaging material, furniture and processed lumber.[2,14,15] Trade of such commodities notoriously facilitates the introduction and local propagation of non-native biota but is often overlooked by ecologists and invasion biologists.[16,17] Despite its vast socio-economic impacts in multiple Asian countries, the (trade-enabled) invasion potential of *B. longissima* has not been comprehensively assessed.

To complicate matters further, even in temperate, first-world settings there is a lack of robust, scientifically based risk assessments for many invasive tree pests.[13,18] Baseline ecological information is often lacking for species of concern, and even relatively straightforward climate suitability analyses have not been conducted for e.g. *B. longissima*. Data on genetic variability, introduction sources and invasion pathways strengthen risk assessments,[19] though these tend to be absent for most invasive species in the developing world tropics. Hence, plant health authorities, pest management professionals and coconut farmers across the Asia-Pacific region lack the necessary scientific insights to forecast future incursions or establish effective quarantine protocols and biosecurity measures.

In this study, we carried out an interdisciplinary assessment of the determinants of *B. longissima* historic spread. First, we collated *B. longissima* introduction records and genetic profiles from several Asian countries to characterize its (trade-mediated) spread pathways. Second, we conducted laboratory assays to determine *B. longissima* biological traits and anticipate its associated invasion potential. Third, we employed climate niche modeling to assess future risk for *B. longissima* invasions across the Asia region and globally. Though invasive pests inflict annual multi-billion dollar losses on South-East Asia's economies,[20] our work is one of the first concerted efforts to illuminate species' invasion pathways, anticipate the invasibility of particular geographies, and thereby strengthen national and regional biosecurity protocols.

2 METHODS

2.1 Distribution records and inter-country palm trade

We collated historic *B. longissima* occurrence records, interception reports and published information in the scientific literature from different Asian countries. For each locality record, we extracted the GPS coordinates and plotted those using GIS software (ArcGIS 10, ESRI, Redlands). For interception records at Chinese ports, we noted the exact date of the interception, name of the port, and source country of the shipment. During 1999–2010, we recorded the annual number of interception records, using baseline information from the Animal and Plant Quarantine Service Information Resources Sharing Platform (http://10.238.254.133/mainwan.asp).[5,6]

Next, we documented all China-bound imports of live palm plants emanating from different South-East Asian countries. The latter data were obtained for the 1999–2010 period, from the China Customs Statistics Yearbook.[21] A Pearson correlation analysis was conducted between the annual (live palm plants) import volume and the number of *B. longissima* interceptions at Chinese ports using SAS software (SAS Institute Inc., Cary, NC, USA).

2.2 Population genetics analyses

To characterize *B. longissima* genetic diversity in its native and invaded range, we field-collected specimens of hispid adults from multiple locations in Vietnam, Indonesia, Thailand, Malaysia and China (i.e. Hainan, Yunnan, Guangdong, Guangxi and Taiwan) between 2004 and 2009. At each site, three to 20 individuals were collected (Table S1), and all specimens were preserved in 95% ethanol and stored at −20 °C. Voucher specimens were kept at −70 °C. Next, we compared sequences from the cytochrome oxidase subunit 1 (COI) gene of mitochondrial DNA (mtDNA) and two internal transcribed spacer (ITS1, 2) regions of nuclear ribosomal DNA. Genomic DNA was extracted using a standard proteinase K/chloroform/phenol extraction protocol.[22] The partial region of the mitochondrial COI gene was amplified using universal invertebrate primers.[23] The PCR primers of Ji *et al.*[24] were used for amplification of internal transcribed spacer 1 regions ITS1 and ITS2. Next, PCR products were examined on 1.5% agarose gels and the expected fragments were purified by using AxyPrepTM PCR Cleanup Kit (AXYGEN, Hangzhou, China). Sequencing was performed in both directions on ABI PRISM 3730 automated sequencer and corrected with SEGSCAPE VERSION 2.0 (Applied Biosystems, USA). Raw nucleotide sequences were assembled using SeqMan (DNAstar package) and sequence information was checked for consistency from both directions manually. All sequences (Table S2) were deposited in Genbank (mtDNA COI gene JQ302134–JQ302190; rDNA ITS1: JQ302014–JQ302071; rDNA ITS2: JQ302072–JQ302133).

Phylogenetic analyses were performed separately for each sequence segment and for all regions in a concatenated dataset by using neighbour-joining (NJ), maximum parsimony (MP) and Bayesian methods using *Diabrotica barberi* (Coleoptera: Chrysomelidae) as an outgroup.

2.3 *B. longissima* life history parameters

We characterized key life history traits of *B. longissima* and compared them with (published data on) other important invasive beetles such as *R. ferrugineus*,[3] *A. glabripennis*[2] and *A. planipennis*.[4] Trials were conducted in controlled environment chambers (A1000, Conviron, Manitoba, Canada) at 25 ± 1 °C, 75 ± 5% relative humidity (RH) and a light and dark period of 12 h:12 h (L:D) using a laboratory colony of *B. longissima*. This colony was established with 350 individuals collected during 2004 from *C. nucifera* palms in Haikou (Hainan, China), and subsequently maintained on *C. nucifera* leaves following Lu *et al.*[25] Basic life history parameters, temperature-related development thresholds (e.g. supercooling point) and flight ability[8,26] of *B. longissima* were determined using methods outlined in the Supplementary Materials.

To assess the effect of host deprivation on *B. longissima* oviposition dynamics, 120 pairs of newly emerged adults were transferred to individual glass vials (0.4 cm diameter, 7 cm long) with a 5-cm section of fresh coconut leaf. All vials were held at 25 ± 1 °C,

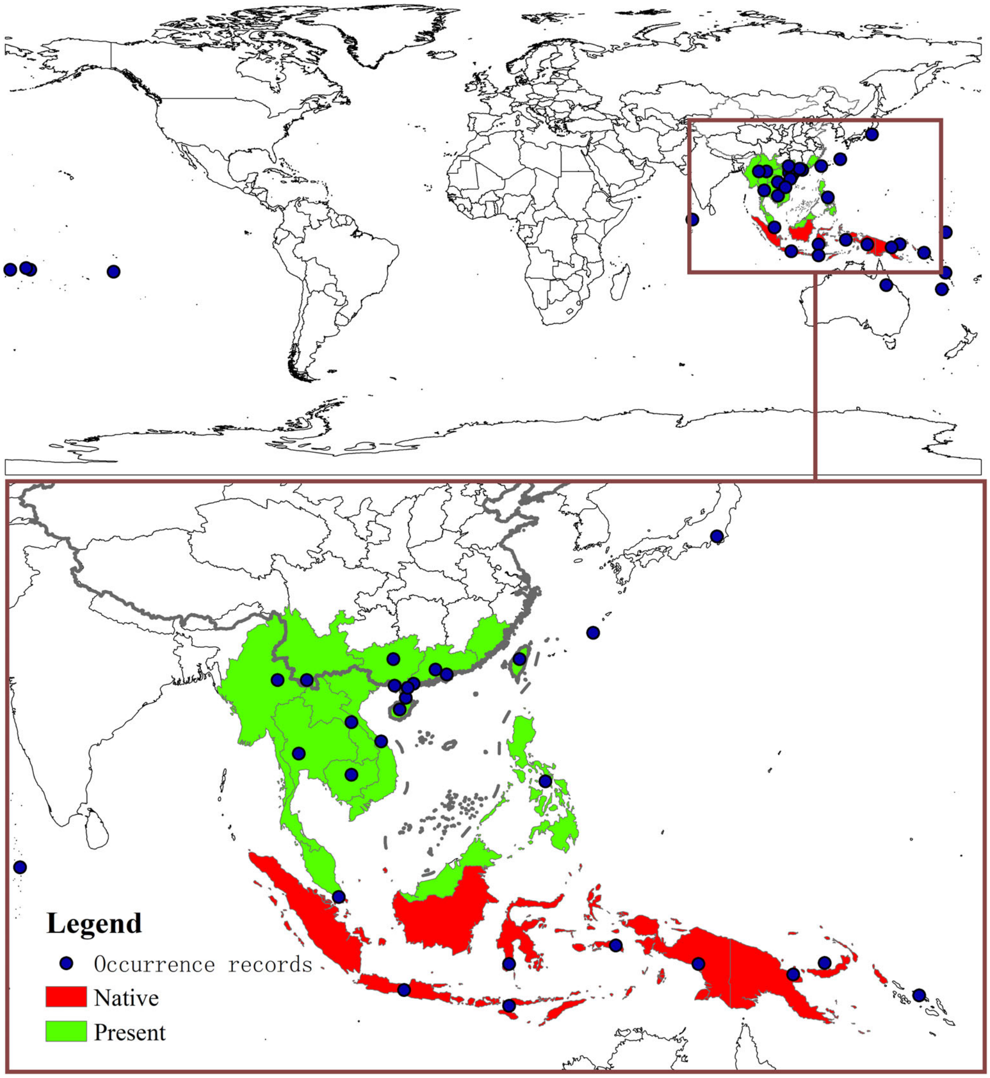

Figure 1. Current geographic distribution of *B. longissima* in South-East Asia. The distribution map is based on historic interception records, occurrence reports and published scientific information.

75 ± 5% RH and a photoperiod of 12 h:12 h (L:D). Sixty pairs were provided with continuous access to leaves while the remaining pairs were deprived of coconut leaves for four consecutive days at days 7, 29, 49, 67, 87, 107. On a daily basis, fecundity (eggs per female) and adult survival were recorded and observations continued until all beetles died. The differences in female longevity, daily and lifelong (total) oviposition were compared between both treatments using Student's *t*-test.

2.4 Climate suitability mapping

Climate-based niche modeling was conducted to determine the geographical extent of climatic suitability for *B. longissima* using the Compare Locations module and the tropical template within CLIMEX (Hearne, Australia).[27] Climatic suitability was expressed with the ecoclimatic index (EI), with EI values below 10 indicating lack of suitability, 10–30 indicating suitability and those above 30 signaling high suitability. The niche model was further parametrized using experimental data on *B. longissima* temperature-dependent development (Tables 2, S3).

Developmental thresholds for *B. longissima* were determined to be 11.10 °C (Table 2), and this value was set as the lower temperature threshold (DV0).The optimum development temperature was 24–28 °C, which allowed the respective lower and upper optimum temperatures (DV1 and DV2) to be set. Under laboratory conditions, *B. longissima* was unable to complete its development at 32 °C, and this temperature was chosen as the upper threshold (DV3). Laboratory trials also allowed the thermal requirement for *B. longissima* development to be estimated as 966.2° days, i.e. development heat demand (PDD). Furthermore, the coconut hispid completes its entire development in the foliage of palm plants, cultivated under tropical conditions in areas with an annual rainfall above 2500 mm.[28] Plant wilting occurs when soil moisture drops below 0.2[29] and this value was chosen as a lower soil moisture threshold (SM0) in the CLIMEX model.

Next, mortality parameters were fine-tuned through a stepwise inductive process by reconciling predicted *B. longissima* occurrence with known distribution patterns. Initial mortality parameters were the laboratory-derived cold development threshold for eggs or larvae (i.e. 10.5 °C). Cold stress is thought to primarily affect *B. longissima* north of the Tropic of Cancer, and its threshold (THCS) was set at −0.01. The upper development threshold *B. longissima* was refined through laboratory assays and set at 38 °C.[30] Lastly,

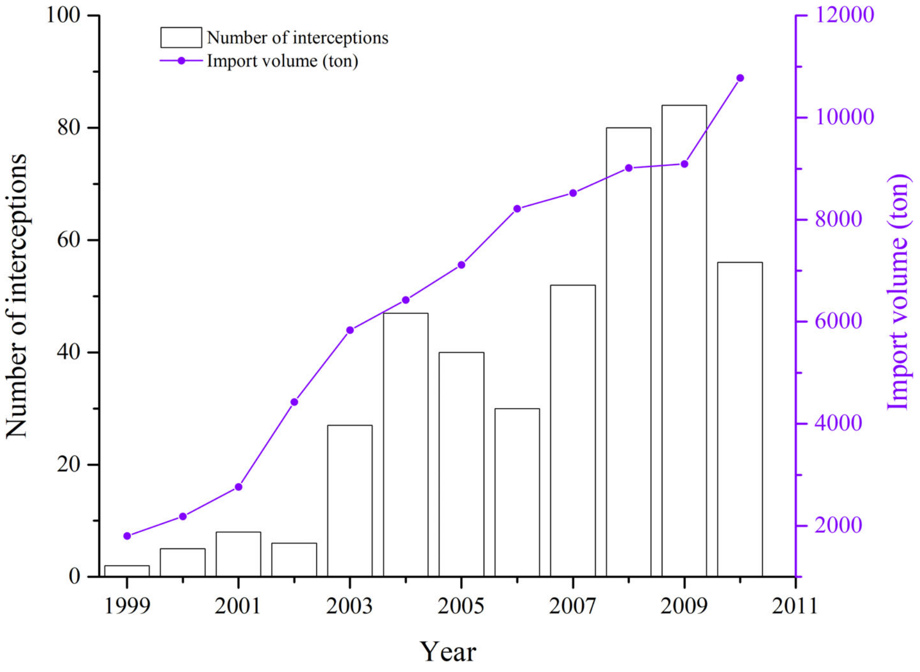

Figure 2. Inter-country trade of live palm plants between China and various South-East Asian countries during 1999–2010 and associated interception records for *B. longissima* at Chinese ports. Annual trade records are expressed in total volume (tons) and capture the number of imported live palms. All data are obtained from the China Customs Statistics Yearbook.

for a heat stress threshold (TTHS), we used 38 °C. Parameter values were adjusted so that heat stress accumulated (THHS) at 0.001 according to the current distribution of *B. longissima* in China.

Lastly, a dry stress threshold (SMDS) was defined according to a dry stress rate (HDS) and calibrated using the *B. longissima* distribution in China. By adapting HDS and SMDS values, the predicted *B. longissima* map was compared to the species' actual in-country distribution. No experimental data were available for wet stress and these parameters were equally calibrated using the species national distribution records, with wet stress (SMWS) set to 1.8 and HDS to −0.002.

Next, EI for *B. longissimi* was plotted and an overlay map was generated using coconut tree distribution areas extracted from the Earthstat web (www.earthstat.org). For selected key coconut-growing countries, the exact area under coconut cultivation was obtained from the UN Food and Agriculture Organization (FAO; www.fao.org) and the annual trade in live trees, plants, bulbs and roots (live plant materials) of the main coconut-planting countries was extracted from the UN Comtrade Database (https://comtrade.un.org/). Using these data, a bubble chart was developed to visualize EI indices for countries with varying degrees of live plant materials trade and coconut cropping area. Furthermore, the average annual import volume of live plant materials trade during 1999–2000 between the invaded countries and uninvaded ones by *B. longissimi* was contrasted using Student's *t*-test.

3 RESULTS

3.1 Geographical distribution and inter-country trade

A total of 29 locality records of *B. longissima* were obtained (Table S1) and its invasion history over the past two decades was plotted (Fig.1). More specifically, *B. longissima* successfully colonized six Asian countries over the 1999–2005 time period. Also, from 1999 to 2010, annual *B. longissima* interceptions at China's ports exhibited a rising trend, parallel to an increased import trade in live palms (Fig. 2, Pearson correlation, $r = 0.87$, $P = 0.0003$).

3.2 Population genetics analyses

Phylogenies of field-collected *B. longissima* showed how genetic profiles of China-collected samples were similar to those from countries in its invaded and native range (i.e. Indonesia; Fig. 3), inferring how *B. longissima* was introduced on multiple occasions from distinct sources within its introduced range (i.e. Malaysia, Thailand and Vietnam) and ancestral area.

3.3 *B. longissima* life history parameters

Fecundity and longevity of adult female hispids was affected by host plant access (Fig. 4), and *B. longissima* females in the host-deprivation treatment had a significantly shorter lifespan than those in the control, with a respective mean value of 119.6 ± 22.2 and 209.7 ± 39.8 (Student's *t*-test, df = 58, $t = 18.1$, $P < 0.01$). Under host-deprivation conditions, total fecundity was significantly lower than under control treatments (112.0 ± 27.7 vs. 208.1 ± 40.7; Student's *t*-test, df = 58, $t = 26.5$, $P < 0.01$), though opposite patterns were recorded for daily oviposition (1.4 ± 0.2 vs. 1.2 ± 0.2 respectively; df = 58, $t = 15.2$, $P < 0.01$) (Fig. 4). Tethered flight trials under laboratory conditions further showed that adult *B. longissima* fly an average of 800 m (Table 1). Generation time and fecundity of *B. longissima* was consistent with that of ten other invasive beetle species (Table 1), and the adult body size and host range of *B. longissima* was equally comparable to that of other invasive beetles (Table 1).

3.4 Climate suitability mapping

Using laboratory-derived biological and ecological parameters (Table 2), the (potential) climate-based geographical distribution of *B. longissima* was determined (Fig. 5). Most of the world's

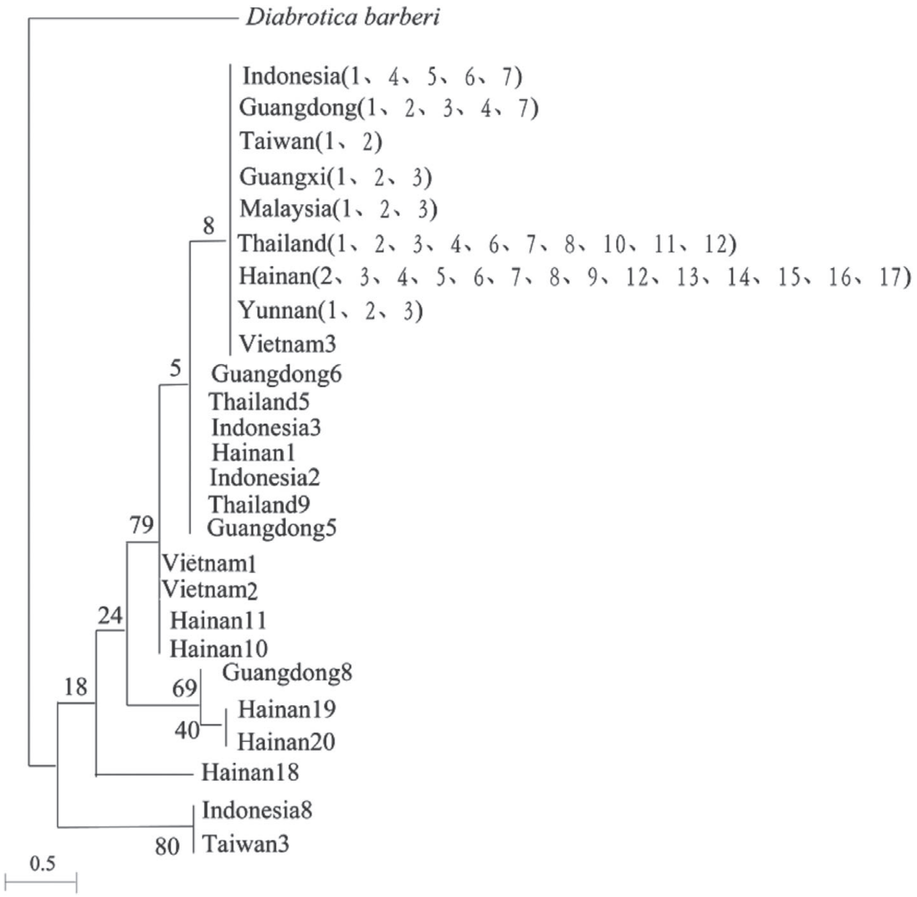

Figure 3. Genetic diversity of *B. longissimi* across the South-East Asia region. Specimens were field-collected between 2004 and 2009 from Vietnam, Indonesia, Thailand, Malaysia, Taiwan and different Chinese provinces. Phylogenetic trees are based on concatenated sequence data from COI subunit 1, ITS1 and ITS2 genes (internal transcribed spacer regions of nuclear ribosomal DNA).

main coconut-growing areas were found to be suitable to highly suitable for *B. longissima*. In Asia, suitable areas with EI indices from 19.1 to 34.0 were delineated in Indonesia, India, Thailand, China, Malaysia, Papua New Guinea, Philippines, Myanmar, Vietnam, Cambodia and Sri Lanka. In the Americas, suitable areas with EI 12.1–63.2 were recorded in Brazil, Venezuela, Colombia, Mexico and Cuba. In Africa, suitable areas had EI indices ranging from 20.5–41.0 and were mapped in the United Republic of Tanzania, Mozambique, Cote d'Ivoire, Ghana, Madagascar, Kenya and Guinea. Several climatically suitable coconut-growing countries imported considerable amounts of live plant materials, with invaded countries importing larger amounts of these commodities than uninvaded areas (invaded 23.93 ± 9.83, uninvaded 1.32 ± 0.75, Student's *t*-test, df = 11 $t = 2.11$ $P = 0.0584$, Fig. 6).

4 DISCUSSION

As a key feature of global change, invasive species have become an issue of worldwide concern,[32] with the pace and geographical extent of biological invasions closely tied to international commodity trade.[33] Invasive insects currently impose a US $70 billion annual burden on the global economy,[34] inflicting disproportionate impacts on (often) ill-prepared emerging economies in the tropics.[35,36] In the Asia-Pacific region specifically, insect invaders pose a well-recognized threat to national economies, human health and the environment,[20] yet their biology, invasion potential and spread pathways regularly remain unstudied. One prominent invader, the coconut hispid *B. longissima*, is a debilitating pest of coconut and other palms, and its earliest (human-mediated) invasion dates from 1929.[63] Here, we accentuate the role of commodity trade in propelling pan-Asian *B. longissima* invasions by describing the genetic profile of invading populations, its favorable biological traits and comparatively weak flight ability, and a close association with (China-bound) trade in live palms.

Genetic diversity of *B. longissima* in its invaded range (including China's Hainan island) is relatively high, suggesting multiple (long-range) introductions as possibly enabled through international trade.[64] This is further supported by an increased number of *B. longissima* interceptions at China's ports since the early 2000s (Fig. 2), parallel to surging imports of live palms, e.g. from Taiwan and Indonesia (1999) or Vietnam (2000).[5] These kinds of interception records are valuable, as they unambiguously identify invasion pathways, allow proper targeting of quarantine protocols or biosecurity measures, and permit early detection of new arrivals.[14,37,38]

Laboratory trials reveal how *B. longissima* exhibits a prolonged oviposition period (average 139.84 ± 2.19, max. 180 days), which benefits establishment and spread in novel settings. This trait also permits early colonists to adjust egg-laying to suit unfavorable or unpredictable environmental conditions. High fecundity coupled with a prolonged oviposition period and adaptable egg-laying behavior plausibly enhances the probability of *B. longissima* to establish persistent populations, even when sporadically deprived of its plant host.[39,65,66] Though variable, the adult body size of

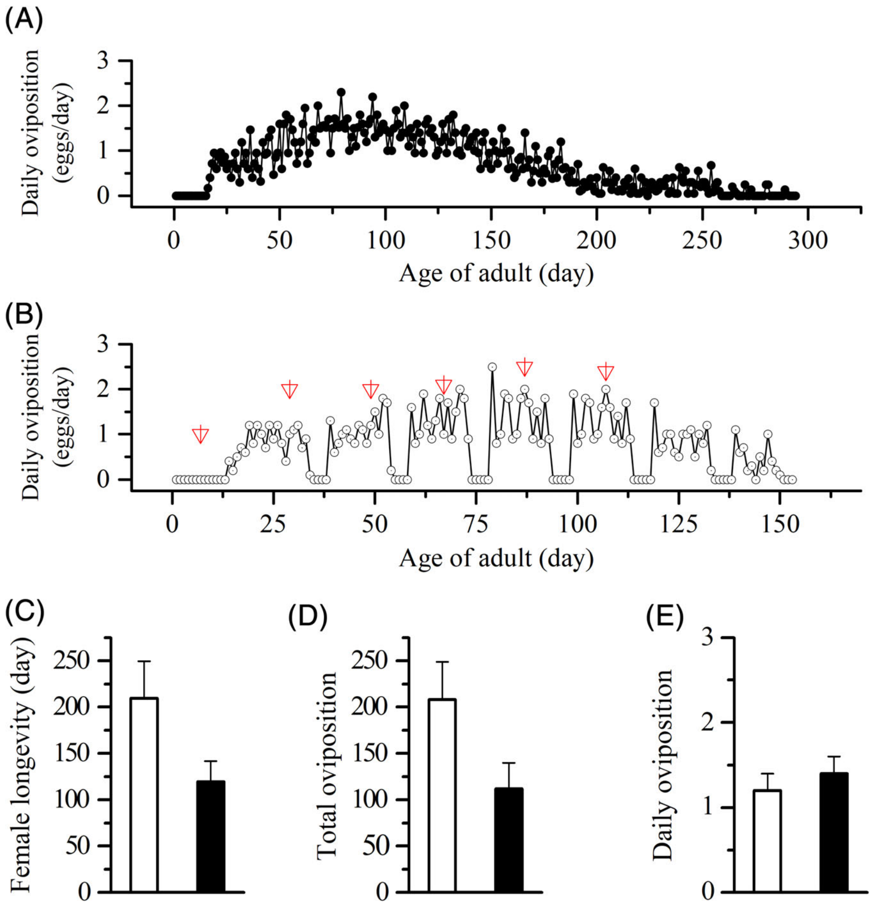

Figure 4. Key life history parameters for *B. longissima*, including longevity and oviposition, under varying access to its plant host. Daily, lifelong oviposition patterns are shown for conditions of (A) continuous and (B) 4-day deprived access to its plant host. The red arrows indicate periods when hosts were not available. (C) Female longevity, (D) total oviposition and (E) daily oviposition are also contrasted between conditions with continuous (open bar) and interrupted (solid bar) access to its plant host. In the latter three graphs, patterns are statistically different between the two host-access conditions (Student's *t*-test, $P < 0.01$).

Table 1. Laboratory-derived life history parameters of *B. longissima*, as contrasted with a number of other species of invasive beetles. Data are reported for a total of ten invasive pests of forests and trees, for which published data on their biology, host range and flight performance could be accessed

Family	Species	Fecundity	Generation time (d)	Body size (mm)	Genera of host plant[b]	Flight ability (km)	Literature ref.[a]
Buprestidae	*Agrilus planipennis*	100	350	12.0	4	0.5	50,51
Chrysomelidae	*Brontispa longissima*	210	190	15.0	9	0.8	
	Pyrrhalta viburni	500	365	6.5	1	1.0	59,60
Cerambycidae	*Anoplophora glabripennis*	239	365	40.0	13	2.0	2,31
	Anoplophora chinensis	200	365	40.0	28	3.0	2,47
	Tetropium fuscum	80	365	17.0	6	9.0	52,53
Curculionidae	*Dendroctonus frontalis*	-	60	3.0	2	3.0	61,62
	Dendroctonus valens	157	365	9.0	5	16.0	54–56
	Rhynchophorus ferrugineus	239	242	34.0	21	1.5	3,48,49
	Scolytus multistriatus	140	180	3.5	1	5.0	57,58
Mean		207.2	284.7	18.0	9.0	4.2	
SD		123.8	109.9	14.6	9.1	4.9	
Coefficient of variation		0.6	0.4	0.8	1.0	1.2	

[a] We consider nine important invasive beetles for which publications were found that describe investigations on their biology.
[b] Data of host range from EPPO web.

Table 2. Biological traits of *B. longissima* when reared on *C. nucifera*

Parameter*	Value
R_0 (net reproductive rate)	54.10
r_m (intrinsic rate of increase)	0.026
λ (finite rate of increase)	1.026
PDT (population doubling time, days)	26.70
DZ (developmental zero or threshold temperature °C)	11.10
K (degree days above the lower threshold for development)	966.20
SCP (supercooling point °C)	−17.10

*Life table parameters were determined at 25 °C with 75 ± 5% RH and a photoperiod of 12 h:12 h (L:D). SCP, flight and time mortality were evaluated using adults.

B. longissima and other invasive beetle species was consistently larger than that of *r*-selected species (e.g. *Bemisia tabaci*). While *k*-selected insects can have a superior establishment success to *r*-selected ones,[26] the comparatively high fecundity, survival rate and (often) dispersal ability of large-bodied beetles may favor invasion processes. Dietary behavior is likely not to be a main determinant of invasion success for beetles such as *B. longissima*, i.e. an oligophagous feeder on palms that attains its highest fitness on coconut.[40] This is also emphasized by its restricted distribution to coconut-growing areas. Though flight performance relates to a species' invasion success,[41] the relatively poor flight capability, i.e. 800 m distance, of adult *B. longissima* does not appear to limit its invasion potential. In conclusion, *B. longissima* possesses numerous traits that aid an effective establishment in novel environments but is a relatively poor disperser, yet the latter is offset by its ability to exploit (anthropogenic) spread of its primary host plants.

Climate-based niche models revealed how multiple coconut-producing tropical countries have suitable climatic conditions for the establishment of *B. longissima*. Amongst these, India, Sri Lanka, Brazil, Mexico and Tanzania have climate-suitability indices of EI 12.7–37.3 with an average of 26.9 in their coconut-growing areas (as compared to 19.5–34.0 with an average of 26.7 in the main invaded range), and thus are at elevated risk of invasion by *B. longissima*. For each of the above nations, potential invasion pathways are different yet can be clearly illuminated. Countries such as India and Bangladesh border *B. longissima*-affected nations and may thus be subject to natural dispersal of the pest, possibly aided by increased climatic variability.[42] Invasion risk in countries such as Brazil or Mexico, however, will depend on long-distance trade of live palms, a well-recognized driver of tree-killing pest invasions.[43] Such a threat can only be counteracted by upgrading country-specific regulations for live plant imports and tightening quarantine and biosecurity measures. Our development of

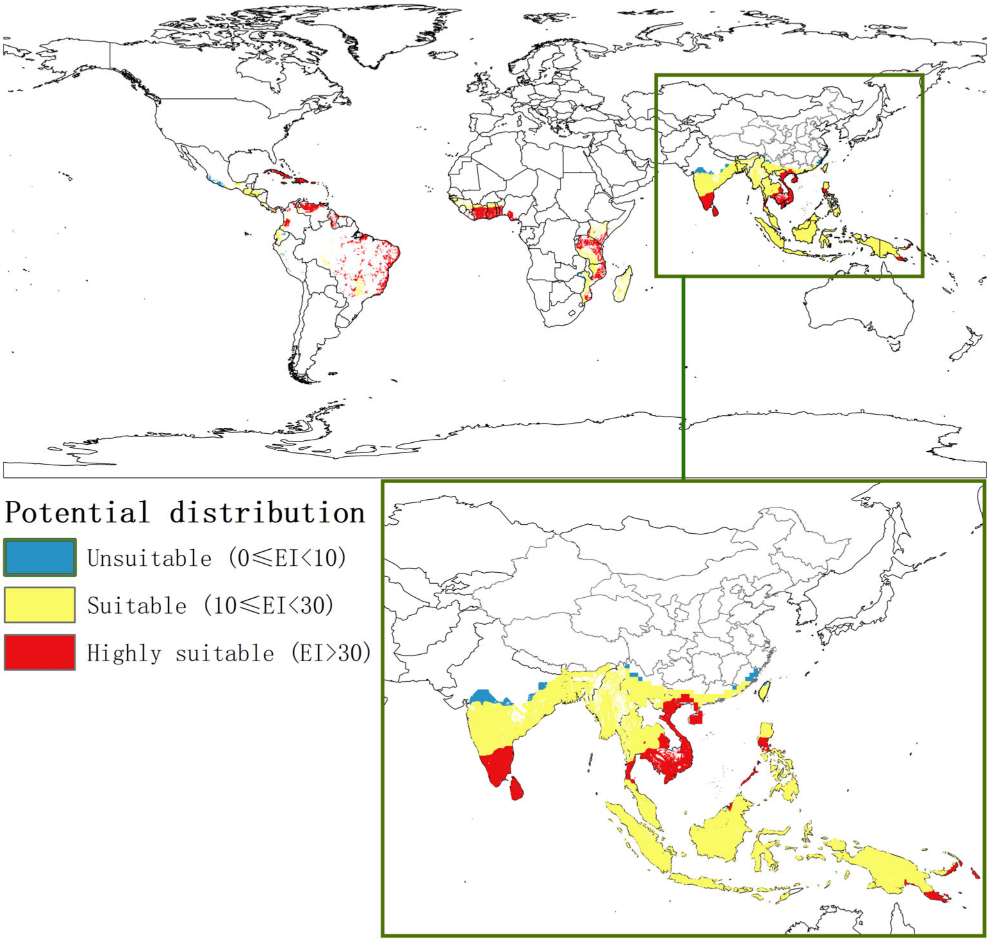

Figure 5. Climatic suitability map for *B. longissima*, with particular reference to the world's key coconut-growing regions. Predictions are based on the CLIMEX-generated ecological index (EI), a measure of the climatic suitability for *B. longissima* scaled from 1–100. Climatic suitability measures are only shown for areas where coconut is presently grown.

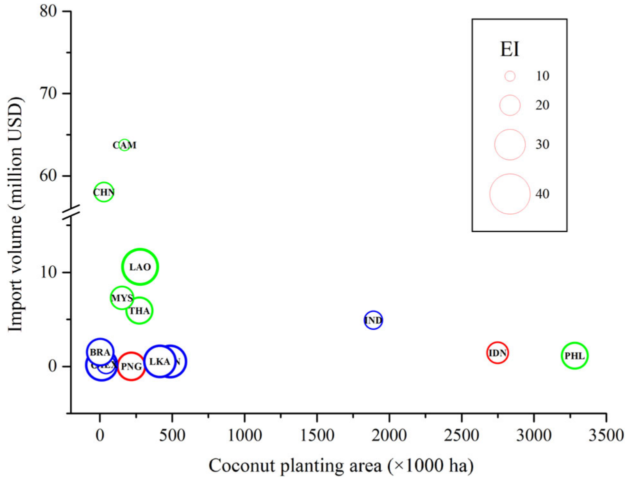

Figure 6. Bubble chart representing potential *B. longissima* invasion risk for key coconut-growing countries. A total of 15 coconut-growing countries are ranked according to their import (value) of live plant materials, coconut planting area and EI. The size of each bubble represents the EI value. Color coding is used to designate *B. longissima* invasion status, with red representing the species' native range, green invaded range and blue (currently) uninvaded countries.

(climate-based) niche models only constitutes a first step in a globe-spanning pest risk assessment for *B. longissima*, and much work remains to be done to generate fine-resolution, credible and useful pest risk maps for this species.[13] These maps ideally contain an added layer mirroring inter-country trade and associated vulnerabilities.[17,44]

In conclusion, our research illuminates how inter-country trade patterns, interception records, species genetics and bio-ecological parameters help to assess *B. longissima* invasion potential. Though the species' high fecundity and prolonged, adaptable oviposition behavior can aid its establishment, China's phytosanitary data reveal a close link with imported live (ornamental, coconut palm) plants, a familiar pattern for several tree-feeding beetles.[9,45] Our work critically assesses the vulnerability of other coconut-growing countries worldwide based on climate-suitability metrics and import trade patterns of live palms, thus providing valuable information to tighten quarantine protocols and other (highly cost-effective) preventative measures.[46] Though limited in scope, this study is a pioneering effort to integrate various types of information (commodity trade, bio-ecology, population genetics data) to map and forecast invasion pathways, comprehensively assess the risk of pest incursions, and thus defuse the globally growing threat of biological invasions.

ACKNOWLEDGEMENTS

This work would not have been possible without the dedicated field work of staff from the Hainan, Guangdong, Guangxi, Yunnan and Fujian Forestry Administration. We also would to thank G. Lovei, M. Zalucki, S. Downes, P. Lai, the late A. Winotai and anonymous reviewers for comments and discussion. This work was financially supported by the Key R&D project in Hainan (ZDYF2017026) and the Central Public-interest Scientific Institution Basal Research Fund for the Chinese Academy of Tropical Agricultural Sciences (1630042017015, 1630042018012, 1630042017011, and 1630042017033).

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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