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Brief Communication

History Does Not Repeat Itself; It Rhymes: Range Expansion and Outbreak of *Plecia longiforceps* (Diptera: Bibionidae) in East Asia

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Abstract

Plecia longiforceps Duda (Diptera: Bibionidae) is reported for the first time from Korea. *P. longiforceps* has been previously known from the East Asian subtropics, south of the 33rd parallel, including southeastern China, Taiwan, and the Ryukyu Islands of Japan. An integrative taxonomic approach based on morphological examination of male genitalia and molecular analysis of mitochondrial cytochrome *c* oxidase subunit I gene sequences confirms the species identification. The recent outbreak of *P. longiforceps* in the Seoul Metropolitan Area, Korea, documented herein represents the northernmost record of this species and suggests its possible range expansion into the temperate zone. Similar to the range expansion and outbreak history of *Plecia nearctica* Hardy (Diptera: Bibionidae) in North America around the Gulf of Mexico in the 1960–1970s, *P. longiforceps* may become a new invasive pest in temperate East Asia. Here, we evaluate range expansion and invasion potential of *P. longiforceps* through Ensemble species distribution modeling and show that a great portion of Northeast Asia and Japan will likely become habitable for *P. longiforceps* in the next 50 years.

Key words: COI barcode, invasive alien species, Korea, lovebug, species distribution modeling

Lovebug Outbreaks

Insect outbreaks are important natural phenomena that have drawn attention from biologists and nonbiologists alike. An outbreak is an explosive increase in the abundance of a particular species that occurs in a short period of time (Berryman 1987), and it can be of particular concern when manifested by an invasive alien species. A sudden appearance of an exotic insect swarm in an urban environment can trigger immediate attention and concern among public health authorities, and animal and plant protection agencies. While the impact of invasive alien species may be evident—as in the case of Asian longhorned beetle on deciduous hardwood forests in the United States (Haack et al. 2010), fall armyworm on maize in Africa (Goergen et al. 2016), or lime swallowtail on citrus groves in the Dominican Republic (Guerrero et al. 2004)—it can also be cryptic with no obvious immediate impact (Venette and Hutchison 2021). Therefore, it is critical to first accurately identify the species in question and evaluate the extent of infestation and potential damage it may cause in invaded areas, including any indirect effects to human health, water, and the environment (Milano and Chèvre 2019).

As one of the most well-documented cases of invasive insect outbreaks, the mass outbreak of the lovebug, *Plecia nearctica* Hardy (Diptera: Bibionidae), in Florida is well known for its unusual scale and impact. Native to Central America and the U.S. Gulf Coast, *P. nearctica* is considered an invasive pest in the southeastern United States (Hardy 1940, Buschman 1976). After the first detection of *P. nearctica* in western Florida in 1949, these lovebugs have been observed in excessive abundance twice a year since the mid-1960s (Buschman 1976). At its peak in 1969, the adult fly swarm was recorded to have covered nearly a quarter of Florida (Hetrick 1970). Due to acidic body fluid that corrodes the clearcoat of automobiles, as well as their potentially adverse impact on apiculture stemming from antagonistic interactions with honeybees, *P. nearctica* is considered a nuisance pest in its introduced range (Leppla 2018, Abou-Shaara et al. 2022).

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In the summer of 2022, an unprecedented outbreak of lovebugs in northwestern Seoul, Korea, sparked concerns among residents and local public health authorities (Fig. 1). Swarming adult flies were observed in abundance, covering streets, building walls, and window screens in densely populated urban neighborhoods, so remarkable that it was featured on national news in Korea (e.g., Im 2022). While lovebugs are not likely to pose any immediate health concerns for humans, these flies are a serious nuisance pest, affecting local businesses due to apparent inconvenience posed by their excessive presence and sanitary concerns. Based on their distinctively rufous thorax, as well as a tendency to occur in massive abundance, these lovebugs were tentatively identified as *P. nearctica* from North America (e.g., Im 2022). However, an accurate understanding of the species identity remains imperative not only to evaluate the extent of risk and threat these lovebugs may pose, but also to unveil the geographical origin of this invaded population, all of which are essential for devising effective pest control measures.

Identification of Lovebugs in Korea

In total, 68 specimens of red-thoraxed lovebugs were collected from the 2022 outbreak and three from 2021, all from the Seoul Metropolitan Area in Korea (Table 1). Our morphological identification based on male genitalia suggested that these specimens are identical to the specimens of *Plecia longiforceps* from Taiwan and the Ryukyu Islands, Japan (Fitzgerald and Nakamura 2015, Tone and Osada 2020, Aoyagi 2022) (Fig. 2 and S2 [online only]). *P. longiforceps* is morphologically most similar to *P. mandibuliformis* Yang & Luo, *P. longifolia* Yang & Luo, *P. stysa* Yang & Chen, and *P. verruca* Yang & Chen, all of which were originally described from southeastern China, and are potential synonyms of *P. longiforceps*, except *P. verruca* (Li 2009). However, the nomenclatural acts proposed by Li (2009) are considered unpublished under Article 9 of the International Code of Zoological Nomenclature (ICZN 2012), and therefore remain to be validated.

Based on mitochondrial COI sequence data, the lovebug specimens from Korea are confirmed to be most similar to those of *P. longiforceps* from Taiwan (see Appendix 1 for detailed methods). All 25 specimens of *P. longiforceps* from Korea are 100% identical in their COI sequences, suggesting their recent establishment potentially from a single invasion. On the contrary, five specimens of *P. longiforceps* from Taiwan show 0–0.46% differences in their COI sequences, even though they were collected by a single flight interception trap at the same locality in 2009. Our neighbor-joining (NJ) phylogeny based on 150 sequences of *Plecia*, together with *Penthetria japonica* Wiedemann (Diptera: Bibionidae) as an outgroup, recovered *P. longiforceps* from Korea as a monophyletic clade with *P. longiforceps* from Taiwan (Fig. 3). Our DNA barcode-based species delimitation using ABGD analysis determined a genetic distance threshold value separating intra- and inter-specific variations to be 5.99% for the 150 *Plecia* sequences, resulting in 15 operational taxonomic units (OTUs), only four of which were given taxonomic names (Fig. 3). These OTUs are further supported in our NJ tree by their reciprocal monophyly.

Systematically, *P. longiforceps* is recovered as most closely related to *P. amplipennis* Skuse (Diptera: Bibionidae) and two other similarly red-thorax *Plecia* OTUs from Australia and Pakistan (Fig. 3, S3 and S4 [online only]). Though the newly established *P. longiforceps* in Korea have been commonly misidentified as *P. nearctica* in various local news reports (e.g., Im 2022), the two species are found to be only distantly-related. Another species of *Plecia* sampled from Korea in this study—*P. thulinigra* Hardy (Diptera: Bibionidae), which can be easily distinguished by its completely black thorax—was recovered as the earliest branching lineage within *Plecia*, sister group to a group composed of the remaining species analyzed.

Range Expansion and Invasive Potential of *P. longiforceps* in East Asia

Our species distribution models predict the present distribution of *P. longiforceps* to be concentrated around subtropical Taiwan, with most part of Japan, Hainan (China), and northern Luzon (Philippines)

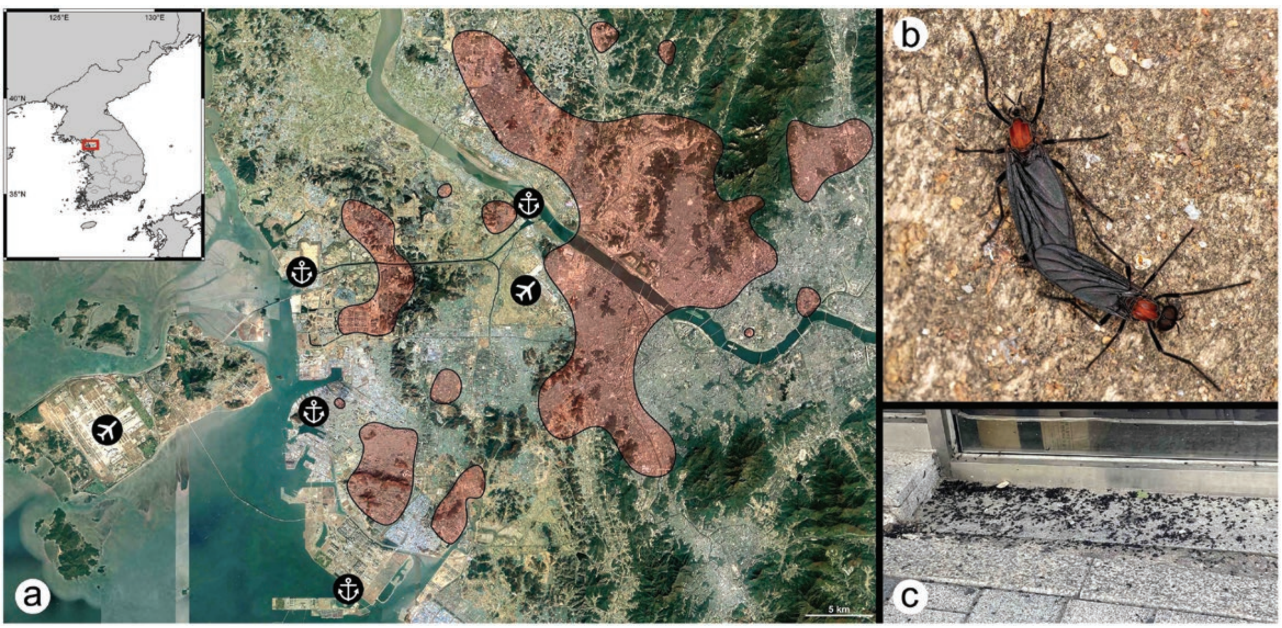

Fig. 1. Observation data of the 2022 *Plecia longiforceps* outbreak in the Seoul Metropolitan Area, Korea: (a) the estimated range of 2022 outbreak with an inset showing a map of the Korean peninsula with the satellite image area marked in red box; (b) a mating pair of *P. longiforceps*; and (c) an example of mass outbreak in urban setting. The satellite image shows that *P. longiforceps* has spread near major ports and airports (marked with respective symbols), and across most urban areas southwest of Bukhansan mountain (elevation 826 m). Map data: Google, Maxar Technologies, CNES/Airbus. Photograph of *P. longiforceps* courtesy of S. Loo.

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Table 1. Summary of *Plecia* specimens used in this study

Taxon name	Collection locality	Collection method	Collection date	No. specimens
P. longiforceps	KOREA: nr. Bukhansan (Mt.) NP, Pyeongchang-dong, Jongno-gu, Seoul; 37° 36.84′ N 126° 57.93′ E, 204 m asl.	Sweeping	27-VI-2021	3
	KOREA: nr. Bukhansan (Mt.) NP, Pyeongchang-dong, Jongno-gu, Seoul; 37° 36.84′ N 126° 57.93′ E, 204 m asl.	Sweeping	5-VII-2022	4
	KOREA: nr. Jichuk Stn., Jichuk-dong, Deokyang-gu, Goyang-si, Gyeonggi-do; 37° 39.10′ N 126° 54.54′ E, 24 m asl.	Sweeping	6-VII-2022	28
	KOREA: nr. Gupabal Stn., Jingwan-dong, Eunpyeong-gu, Seoul; 37° 38.25′ N 126° 55.04′ E, 77 m asl.	Sweeping	15-VII-2022	36
	TAIWAN: Nanren Road, Nanrenshan (Mt.), Manzhou Township, Pingtung County	Flight interception trap	21-VI~4-VII-2009	5
P. thulinigra	KOREA: Yongdae Nat. Rec. Forest, Buk-myeon, Inje-gun, Gangwon-do; 38° 14.74′ N 128° 19.99′ E, 595 m asl.	Malaise trap	7-VI~1-VII-2021	1
	KOREA: Taehwasan (Mt.), Docheok-myeon, Gwangju-si, Gyeonggi-do; 37° 18.43′ N 127° 18.32′ E, 153 m asl.	Malaise trap	10-V~15-VI-2022	1
	KOREA: nr. UNIST, Banyeon-ri, Eonyang-eup, Ulju-gun, Ulsan; 35° 34.683′ N 129° 11.307′ E, 77 m asl.	Malaise trap	26-V~14-VI-2022	3
	KOREA: Wolchulsan (Mt.) NP, Gunseo-myeon, Yeongnam-gun, Jeollanam-do; 34° 45.223′ N 126° 40.087′ E, 157 m asl.	Malaise trap	28-V~22-VI-2022	5

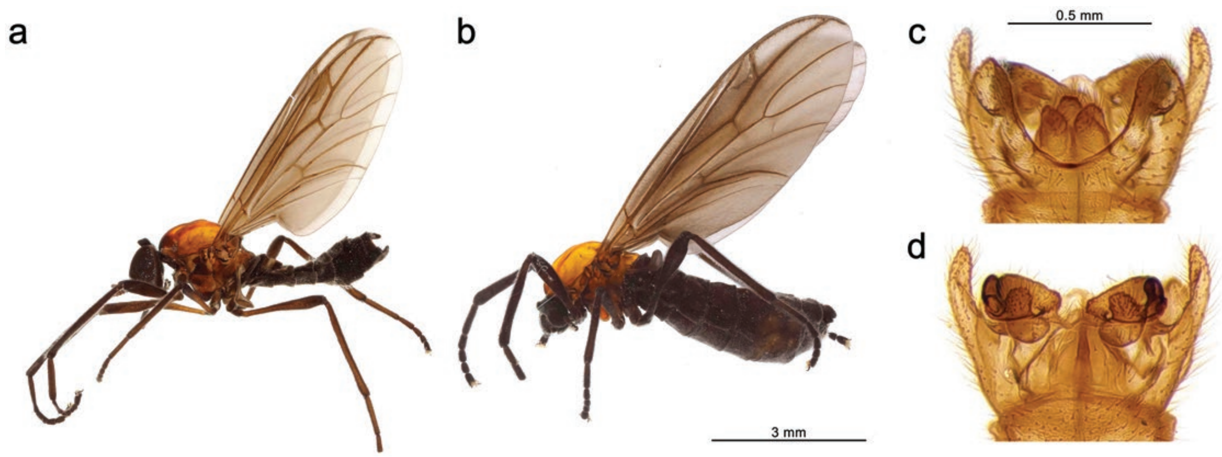

Fig. 2. *Plecia longiforceps* from Korea: (a) male habitus; (b) female habitus in lateral view; (c) male genitalia in dorsal view; and (d) male genitalia in ventral view.

to be highly habitable for this species (Fig. 4; see Appendix 1 for detailed methods). In contrast, most continental areas of its current range in southeastern China and Korea are found to be suboptimal. Specifically, the Seoul Metropolitan Area—from which the outbreak of *P. longiforceps* in the temperate region is reported here for the first time—is not recovered as a high-probability region, highlighting the importance of the observed establishment. Outside of its native range in southeastern China and Taiwan, *P. longiforceps* was recently reported from the Ryukyu Islands with the oldest collection material dating back to 1996 (Fitzgerald and Nakamura 2015). Following the initial report from the Japanese islands of Yaeyama, situated in close proximity to Taiwan (Fitzgerald and Nakamura 2015), *P. longiforceps* seems to have spread northeastward, reaching Okinawa Island prior to 2015 (Tone and Osada 2020, Aoyagi 2022).

The future range of *P. longiforceps* based on six scenarios of climate change unequivocally shows an expansion of the total areas suitable for *P. longiforceps* by 2070, particularly across Korea and eastern China (Fig. 4). With the anticipated range expansion of *P. longiforceps* in East Asia, the establishment of this species in Korea is significant for its likely origin through a long-distance dispersal, as well as for its first instance in the temperate zone. As the present distribution of *P. longiforceps* within Korea is restricted to the Seoul Metropolitan Area around major ports and airports—where regular arrivals of goods and passengers from China, Taiwan, and Japan are present (Fig. 1), the introduction of *P. longiforceps* into Korea is presumably anthropogenic in origin through horticultural commodities and international travelers. In fact, the larvae of many soil-dwelling march flies, such as *P. nearctica* in Florida and *Bibio nigriventris* Haliday (Diptera: Bibionidae) in Moscow, have been reported to have spread in soil or turf by humans (Buschman 1976, Krivosheina et al. 2019). A growing number of tropical and subtropical invasive pests have been reported to have established at major port cities across Korea in recent years (e.g., Kang et al. 2017, Mohamadzade Namin et al. 2019, Byeon et al. 2020, Lee et al. 2020), which may be attributable to increase in global trades, in conjunction with ongoing climate change (Hong et al. 2012).

The observed pattern in both the present and future range of *P. longiforceps* indicates that this species prefers oceanic climate with high humidity. Given that the entire area of southern Japan is extrapolated as a high-probability region for *P. longiforceps*

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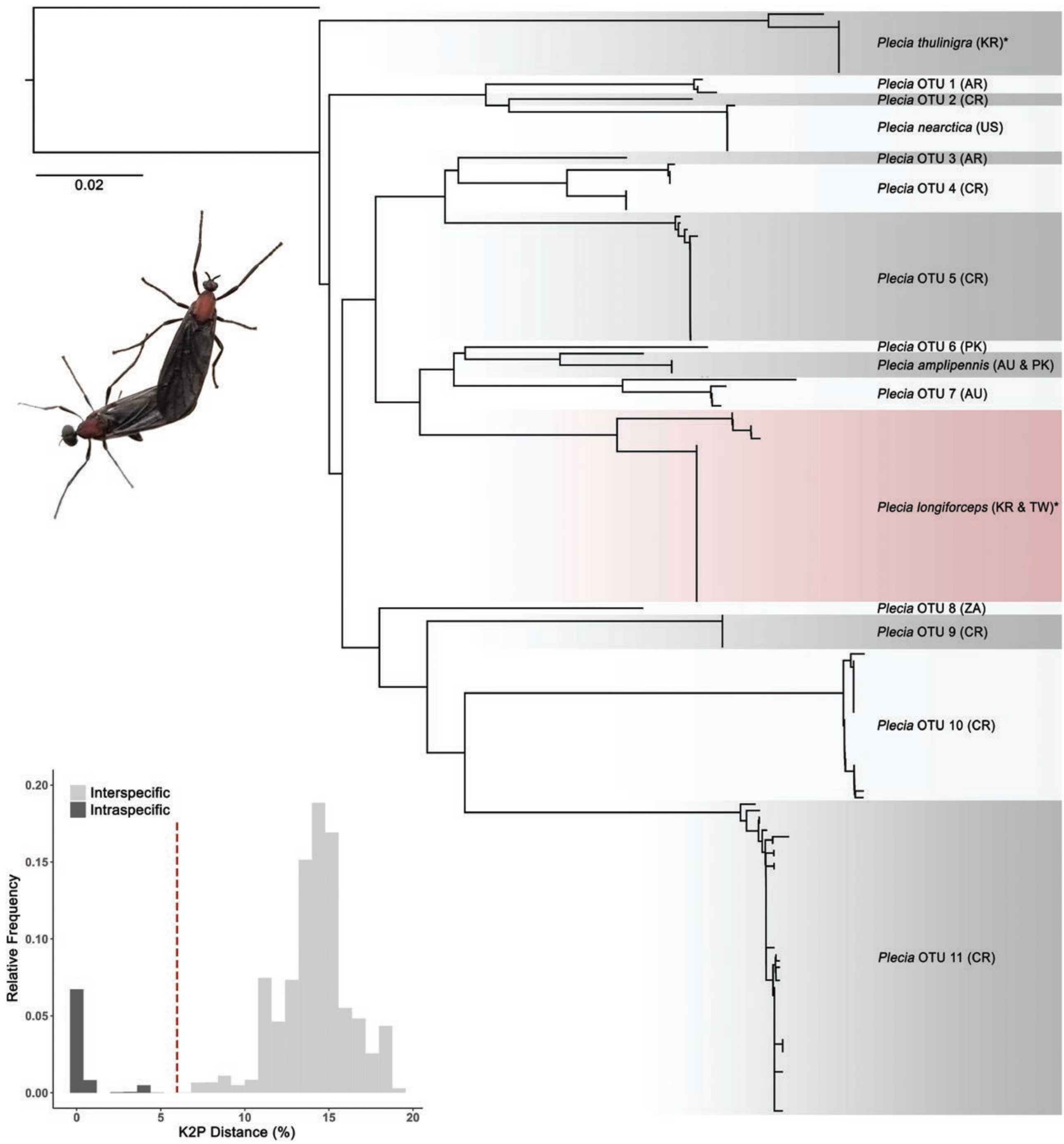

Fig. 3. Neighbor-joining (NJ) tree of *Plecia* based on 151 COI sequence data. Each shaded clade represents distinct species or operational taxonomic unit (OTU) as determined by DNA barcoding analysis, with the red shade highlighting *P. longiforceps* from Korea and Taiwan. Clade label consists of taxon name or OTU numbers and collection locality in ISO Alpha-2 country code. Species newly sequenced in the present study are marked with asterisk. The barplot shows the pairwise distribution of 151 sequences analyzed. The dotted redline in the barplot represents the genetic distance threshold value (5.99%) determined by ABGD that separates intra- (dark grey) and inter-specific (light grey) sequences. *P. longiforceps* photo courtesy of H. Kang. Detailed tip information is available in Supp Fig. S3 (online only).

(Fig. 4), it is conceivable to interpret the recent outbreaks of *P. longiforceps* in the Ryukyu Islands as evidence of an ongoing range expansion into Japan via repeated short-distance dispersal across the island chain as a stepping-stone. Because the climate conditions in Japan at both the present and future are highly favorable for *P. longiforceps*, a mass outbreak of *P. longiforceps* is expected once this species gets established in the main islands of Japan. It is worth noting that the introduced populations in the subtropical Ryukyu Islands show nuptial flights twice a year in spring and fall (Fitzgerald and Nakamura 2015, Tone and Osada 2020), which is in accordance with Duda (1933) who noted that collections were made in May and September in southeastern China. However, the population newly discovered from Korea occurs in abundance only once in late June to early July, highlighting the plasticity of *P. longiforceps* with its seasonality and voltinism depending on the climate conditions.

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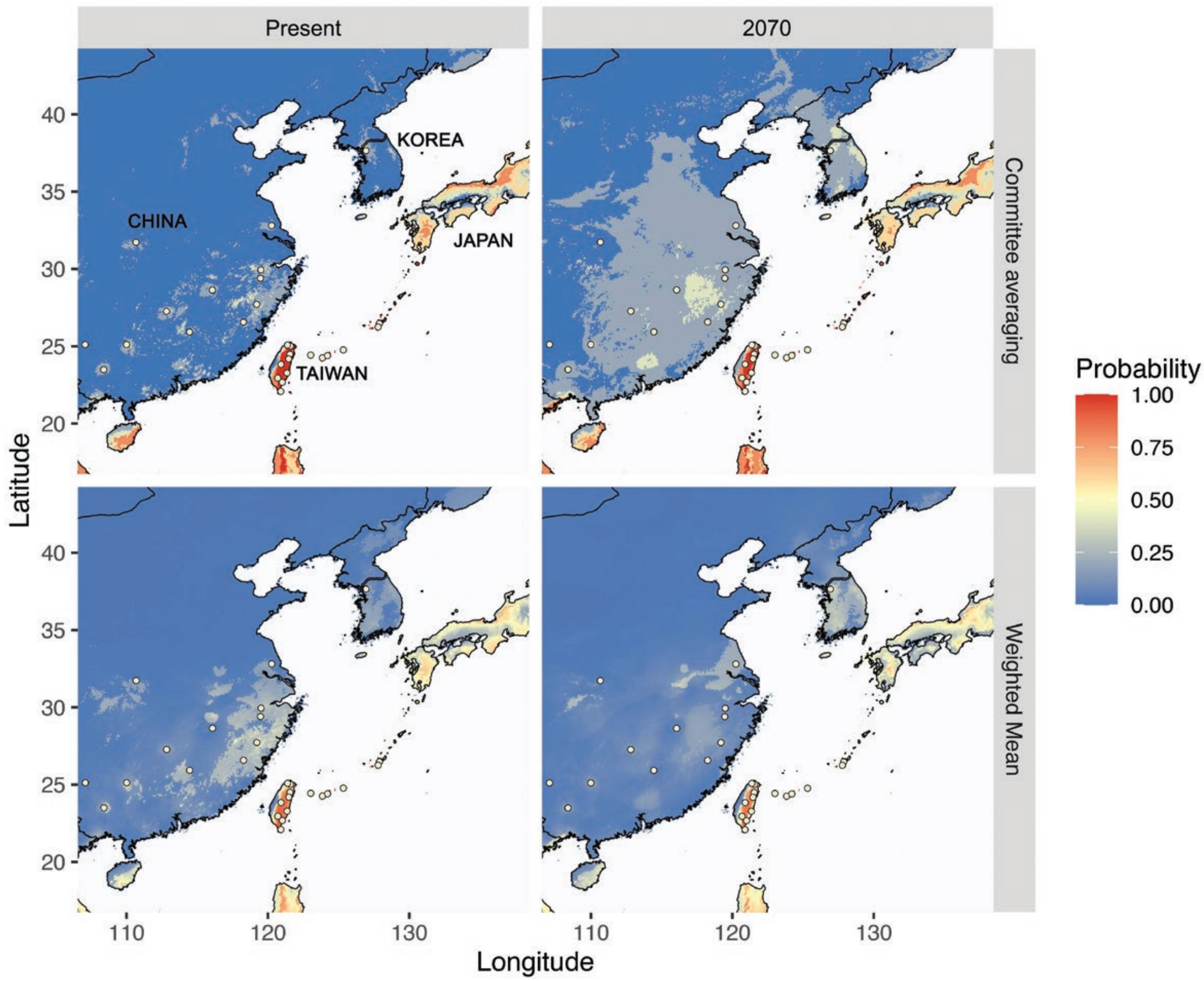

Fig. 4. Projections for the distribution of *Plecia longiforceps* in East Asia at present and in 2070 under Ensemble species distribution model.

The observed dispersal and range expansion of *P. longiforceps* in East Asia is comparable to the well-known case of *P. nearctica* in the southeastern United States. *P. nearctica* was originally recorded from the coastal zone of the Gulf of Mexico from Costa Rica to Louisiana, USA, and has since expanded its range eastwards into Florida and South Carolina (Hardy 1940, Buschman 1976). After the first record of *P. nearctica* from Florida in 1949, massive outbreaks were observed in the 1960–1970s, and continue to occur twice a year in April–May and August–September to date. Although the abundance of *P. nearctica* has not been closely monitored in recent years, swarms as extensive as those reported in the 1970s have not been observed since, and the overall outbreaks have attenuated with some local fluctuations (Leppla 2018). However, with the ongoing climate change, there remain concerns for a possible range expansion of *P. nearctica* into other parts of the United States, where massive outbreaks and their adverse influence on local pollinators seem unavoidable (Abou-Shaara et al. 2022).

The outbreaks of *P. nearctica* in the 1960–1970s have been speculated to be related to its introduction into new habitats in Florida (Buschman 1976), as apparently occurs with many invasive species when environmental resistance is lifted (Venette and Hutchison 2021). *P. longiforceps* in Seoul and Okinawa may undergo similar stages, where populations increase rapidly for a short period and stabilize over time. Urban environments can also contribute to more intense aggregations. *P. nearctica* is known to be attracted to automobile fumes, heated asphalt, and brightly painted buildings (Callahan and Denmark 1973, Callahan et al. 1985), and the moist grasslands of parks, gardens, and highway subgrades can provide suitable habitats for larvae (Hetrick 1970, Krivosheina et al. 2019). Long-term observational studies are required to evaluate the course of establishment of *P. longiforceps* populations in East Asia; however, the observations from Seoul and Okinawa, as well as our species distribution modeling results collectively suggest that *P. longiforceps* will likely spread across the greater part of East Asia, partly aided by anthropogenic factors, becoming a significant invasive pest in their introduced regions. Documenting early stages in the spread of invasive species such as this one can provide critical insights for understanding and predicting longer-term impacts, of particular importance for those species relevant to the animal and plant health agencies or to public health.

Supplementary Data

Supplementary data are available at *Journal of Integrated Pest Management* online.

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Conflict of Interest

The authors declare no conflict of interest.

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