

First Record of *Leptocybe invasa* Fischer & La Salle (Hymenoptera: Eulophidae) males from Uruguay

Carolina Jorge

`carolina.jorge@cut.edu.uy`

University of the Republic

Edson L.L. Baldin

Universidade Estadual Paulista (UNESP). Campus de Botucatu

Carlos F. Wilcken

Universidade Estadual Paulista (UNESP). Campus de Botucatu

Short Report

Keywords: Eucalyptus, Sexual reproduction, blue gum chalcid wasp, Forest health

Posted Date: March 23rd, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8379020/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at International Journal of Tropical Insect Science on September 22nd, 2026. See the published version at <https://doi.org/10.1007/s42690-026-02027-7>.

Abstract

The blue gum chalcid, *Leptocybe invasa* (Hymenoptera: Eulophidae), is one of the main invasive insect pests on *Eucalyptus* nurseries and plantations worldwide. It has been responsible for great losses to forestry companies, associated with the halting of forestry activity, replacement of genetic material, and the discarding of highly susceptible commercial clones. Thelytokous parthenogenesis is the most important reproductive mechanism because males are scarce and their function is unknown. *L. invasa* has been present in Uruguay since 2011, but in February and March of 2019, only females were observed. The objectives of this work are to report for the first time the presence of *L. invasa* males in Uruguay and to analyze the importance of this fact for the country. During 2018 and 2019, collections of branches with *L. invasa* galls were made in several departments of Uruguay. In three vials with *L. invasa* samples from February and March 2019, we observed six males. The samples were from three localities of the Tacuarembó department. The female proportion was 0.99, 0.95, and 0.94, respectively, similar to those observed in Argentina. Future studies should be focused on the *L. invasa* male function in the species' fitness to adapt to a new host. To study whether there is a seasonality in the emergence of the blue gum chalcid wasp males and their impact on these pest management strategies.

Introduction

Eucalyptus plantations represent a relevant source of Fiber for the global pulp and paper industry (FAO 2024). Forest production is one of the main economic activities for Uruguay, where *Eucalyptus* species are the most planted (85%) (DIEA-MGAP 2024). One crucial aspect of the adoption of this genus as a main source of pulp in the beginnings of the pulp industry worldwide was the relative absence of debilitating insect pests and diseases (Wingfield et al. 2008; Rodas & Wingfield 2021). In the last decades, however, this situation has changed with the occurrence of several new pests (insect and pathogens) records (Paine et al. 2011; Hurley et al. 2016). These impacts negatively affect the forest productivity and cause economic losses (Csóka et al. 2017; Meurise et al. 2019).

The main sources of eucalypt pests are the localities where it is naturally distributed (Wingfield et al. 2008). The new records of invasive pests have been related to the increase in the planted areas, the low genetic diversity of the stands resulting from clonal forestry, as well as the global traffic of people and goods (Gibson et al. 1980; Paine et al. 2011; Garnas et al. 2016; Meurise et al. 2019). Notably, the last wave of world-invasive pests in *Eucalyptus* has included small, cryptic insects such as gall-forming species (Hurley et al. 2016; Roques et al. 2016; Dittrich-Schröder et al. 2018).

The blue gum chalcid *Leptocybe invasa* Fischer & La Salle, 2004 (Hymenoptera: Eulophidae) is the most relevant gall-forming species within *Eucalyptus* (Paine et al. 2011; Mendel et al. 2017). This species is considered the main gall-inducing insect pest in greenhouses and plantations of *Eucalyptus* spp. worldwide, given the severity of the attacks and their high capacity for colonizing new environments (Csóka et al. 2017; Otieno et al. 2019; Jorge & Molina 2020). In fact, in just a decade since it was first recorded in Israel, *L. invasa* has succeeded in establishing itself in all the continents where *Eucalyptus* is

planted for commercial or ornamental use (Wilcken et al., 2015a; Jorge et al. 2016; Csóka et al. 2017). In South America, it was first reported in Brazil in 2008 (Costa et al. 2008), in Argentina in 2010 (Aquino et al. 2011), reaching Uruguay in 2011 (Jorge et al. 2016), Paraguay in 2012 (Benítez-Díaz et al. 2014), and Chile in 2014 (SAG 2014).

The blue gum chalcid was first described by Mendel et al. (2004) as a monotypic taxon and a uniparental, because only females have emerged from the *L. invasa* galls collected in Israel, Algeria, Kenya, Spain, and Syria. Subsequently, Doğanlar (2005) reports for the first time the emerged males from galls on *E. camaldulensis* from Turkey and describes them. The abundance of *L. invasa* males found by this author was very low (0.75%), with a sex ratio biased to females, with a female proportion of 0.99. For this reason, thelytokous parthenogenesis is considered the main reproductive mechanism for this pest.

Subsequently, the presence of *Leptocybe invasa* males has been reported in other countries from South America, Africa, Europe, Oceania, and Asia (Chen et al. 2009; Kumari et al. 2010; Akshtar et al. 2012; de Souza 2016; Aquino et al. 2019). Taking into account that the population is skewed towards females, the increase in the male's presence has generated interest in understanding their function for the species' fitness. In samples from surveys of the presence of *L. invasa* galls carried out in February and March 2019, males of the pest were found.

Therefore, the main objective of this work is to report for the first time the occurrence of males of the pest in Uruguay and discuss the implications of their presence for forestation.

Material and methods

Leptocybe invasa galls has been regularly sampled in Uruguay since its first record in 2011 in the main forestry zones of the country (Jorge et al. 2016). For this work, we studied three 20 ml vial samples from Tacuarembó in addition to the emergence of the blue-gum chalcid wasp females; the presence of some males was recorded (Fig. 1). This is something that until now had not been observed in our country (Table 1). The Female proportion (F%) was calculated by $\Sigma \text{♀} / \Sigma (\text{♀} + \text{♂})$, and the sex ratios (SR) were calculated as: $\text{SR} = (\text{♂ number} / \text{♀ number})$ such as in Zheng et al. (2017).

The exemplars examined were all from the Tacuarembó department, in Uruguay (Fig. 1). On *E. grandis* x *E. camaldulensis* plantation near Manuel Diaz (31°35'11.64" S, 55°43'23.10" W), which recorded 3 ♀/ 843 ♂ (F% = 0.99, SR = 1/281) (18/ii/2019). Forest nursery in Tacuarembó city (31°44'30.85" S, 56° 1'4.95" W) in *E. tereticornis*: recorded 1 ♀/ 20 ♂ (F%= 0.95, SR = 1:20) (02/iii/2019). A wind shelter of red gums in Tacuarembó city (31°44'24.87" S, 55°58'48.49" W): 2 ♀/ 32 ♂ (F%= 0.94, SR = 1:16) (26/ii/2019).

All wasps were observed under a stereoscopic microscope Zeiss Stemi DV4. Identification of males was made by observing antennae and abdominal characteristics according to Doğanlar (2005). Voucher specimens were kept in the Forest Entomological Collection of the Laboratorio de Manejo integrado de insectos forestales, Sede Tacuarembó, CENUR Noreste, Udelar, in Tacuarembó, Uruguay.

Results

We observed six *L. invasa* males and 895 females; this constitutes the first record of males for our country (Table 1). The sexual ratios were SR = 1: 281, SR = 1:20, and SR = 1:16, the female proportion was 0.99, 0.95, and 0.94, respectively.

Table 1
Countries where *Leptocybe invasa* males were reported. WD = without data

Continent	Country	Year of the first record	Reference
Asia	China	2009	Chen et al 2009; Zeng et al., 2014a, 2018
	India	WD	Ankita and Poorani (2009)
			Akhtar et al. (2012).
		2009	Kumari et al., 2010
	Laos		Thu et al., 2009;
		WD	Lee et al., 2018
	Malaysia		Lee et al., 2018
	Sri Lanka		Udagedara & Karunaratne, 2014
		WD	Lee et al., 2018
	Taiwan	2010	Tung et al., 2010
	Thailand	WD	Sangtongpraow et al., 2011
Africa	Ghana		Lee et al., 2018
Europe/Asia	Turkey	2004	Doğanlar, 2005
Europe	Malta	WD	Lee et al., 2018
Oceania	Australia	WD	Lee et al., 2018
South America	Argentina	2018	Aquino et al., 2019
	Brazil	2015	De Souza, 2016
	Paraguay	2022	Mota et al. 2025
	Uruguay	2019	New record

Leptocybe invasa male diagnosis

Leptocybe invasa males' diagnosis was made based on Doğanlar (2005), Zheng et al. (2014 a), Aquino et al. (2019), and from our observations.

Males are smaller than females, with 0.8–1.2 mm in length, and females 1.1–1.4 mm. In turn, males are similar in body coloration to females but distinguished by dark brown with a metallic blue-green sheen on the head and mesosoma (Fig. 2A-B). The antennae are yellow-pale in the scape and pedicel, darkening towards the apex and dorsally, funicle and club yellow to light brown (Fig. 2C). Legs are pale yellow except in the middle, and hind coxae and hind femur are brown with a metallic shine (Fig. 2B). The wings are hyaline with light brown veins, and the forewings are without postmarginal veins (Fig. 2. D). Metasoma is as long as mesosoma. A difference with the female antennae is that the funicle is longer and presents four segments, not three. Antennae with long setae beginning at the funicle and continuing at the club (Fig. 2. C). The abdomen is elongated with the aedeagus in the apex, with the digitus having one claw (Fig. 2E).

Discussion

This study reports for the first time the presence of males emerging from *Leptocybe invasa* galls collected in *Eucalyptus* plantations and wind shelters in Uruguay. Although *L. invasa* reproduces usually by thelytocal parthenogenesis, which implies a female-biased sex ratio (Doğanlar 2005), males of this species have been previously reported from Australia, Turkey, two countries in South America, seven from Asia, and one from Africa, and Europe (Table 1). Therefore, the presence of many of the species in our country implies increased attention to the possible implications in the management of this pest species.

Populations of *L. invasa* have different sex ratios (SR) around the world over their geographic distribution (Nugnes et al. 2015). The first description of the males of this insect pest by Doğanlar (2005) showed that these are rare in Turkey (SR: 0.99). Similar results were found in India (SR: 0.99; Akhtar et al. 2012) and Argentina (SR: ≥ 0.96 ; Aquino et al. 2019). In other countries, such as China and Thailand, slightly different results were observed. While in some regions of China (Fujian, Guangdong, Hainan, Guangxi, Jiangxi, and Sichuan), a low proportion of males was reported (sex ratio ≥ 0.95) (Zheng et al. 2017), in others, a high proportion (18–48%) of them was observed (Liang et al. 2010; Nugnes et al., 2015). On the other hand, in Thailand, a higher proportion of males was observed, with a sex proportion of females per males of 1.97:1 (Santongprow et al. 2011). Mota et al. (2025) found 38 females per male in a study in Paraguay. Similarly, we found a female-biased sex ratio in the three sites where we found males (SR: ≥ 0.98).

In Uruguay, the emergence of *L. invasa* females has been observed throughout the year except in cold months, with three peaks: August-September, mid-December, and March-April (Jorge 2019, Jorge et al., in preparation). In this study, we confirm the emergence of males at least during February and March in samples from the year 2019. The question remains whether the emergence of males follows the same seasonality as that of parthenogenetic females. The effect that changes in environmental variables (temperature, humidity, and photoperiod) have on reproductive strategies and the sexual ratio of progeny in hymenopteran species is known (Heimpel & de Boer 2005). Zeng et al. (2017) observed that although females emerged throughout the year with peaks in the warmest months in China, no seasonality was

observed in males. Studies carried out by Zeng et al. (2018) did not observe an effect of temperature and photoperiod on *L. invasa* reproduction tactics or in their offspring sex ratio under laboratory conditions.

Parthenogenesis is common in insects (Vershina & Kuznetsov, 2016). Thelytoky is particularly the most extended type of parthenogenesis among the Hymenoptera (Heimpel & de Boer 2008). Usually, this phenomenon is connected to the occurrence of endosymbionts (Stouthamer et al. 2010; Gualtieri et al. 2017). However, Nugnes et al (2015) suggest that *L. invasa* would reproduce by telythock parthenogenesis due to the presence of the *Rickettsia* spp. endosymbiont. Until now, it is considered that *L. invasa* would reproduce primarily asexually by telythock parthenogenesis and occasionally by sexually with an increase in male emergence (Zeng et al., 2018). According to molecular analysis reported by Nugnes et al. (2015) and Ditttrich-Schröder et al. (2018), *L. invasa* exhibits a low genetic diversity that may be explained by thelytoky. Besides Zeng et al. (2014a), considered that the ability to reproduce by thelytokous parthenogenesis and by sexual reproduction is one of the main causes of their worldwide rapid dispersion. Sexual reproduction constitutes a source of variability (Felsenstein 1974; Misevic et al. 2006; Vershinina & Kuznetsov 2016), contributing to the occurrence of new genotypes to be tested by natural selection.

Hence, the occurrence of males of *L. invasa* increases the chances of this species to adapt to the new environment, including the exploitation of new *Eucalyptus* species or genotypes (Zheng et al., 2014a, b). Thus, the occurrence of males of *L. invasa* in Uruguay should be taken into account when assessing the risk this pest poses to the *Eucalyptus* plantations in the country. Other insect pests such as the bronze bug *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae) or the lerp psyllid *Glycaspis brimblecombei* (Hemiptera: Aphalaridae), both exhibiting sexual reproduction, have adapted quite fast to developing on several eucalyptus species (Saavedra et al. 2015; Wilcken et al., 2015b). For instance, *T. peregrinus* can develop on 42 *Eucalyptus* and *Corymbia* spp. and more than seven hybrid species (Saavedra et al., 2015), whereas *G. brimblecombei* can exploit around 22 host species (Wilcken et al., 2015b). Nadel and Slippers (2011) assessed susceptibility and tolerance by *L. invasa* on 21 species and five hybrids. After a decade, the number of *Eucalyptus* species susceptible to this pest has increased to 37 species and hybrids that have been reported as potential hosts for *L. invasa* (Jorge, 2019).

Concluding remarks, this is the first record of males of *L. invasa* for Uruguay. This finding, together with the growing records of male emergence in other parts of the world, should be considered thoroughly. Although the function of males in this species is not fully understood yet, the presence of these could be associated with sexual reproduction and the increase in the capacity to adapt to new genotypes.

Future studies should be focused on the *L. invasa* male function in the species' fitness to adapt to a new host. To study if there is a seasonality in the emergence of the blue gum chalcid wasp males. Also, whether the increase in the emergence of males can be associated with climate change. It also has implications for pest management in Uruguay and in other countries where *L. invasa* is present.

Declarations

Acknowledgments

The authors want to thank the collaboration of the Sociedad de Productores Forestales (SPF), particularly MSc. Paola Molina and Tec. For. Juliana Ivanchenko from LUMIN. Also, to Lucio Arbiza from the Sede Tacuarembó Udelar for their help during the process and review of *Leptocybe invasa* gall samples collected from the field.

Authors' contributions

C.J. (Carolina Jorge), E.B (Edson L.L. Baldin), and C.W (Carlos F. Wilcken) jointly conceived and designed the study; C.J. wrote the initial draft of the manuscript, searched, prepared the figures, and compiled the final data; C.J., C.F. co-wrote the final manuscript. C.J. and C.F. have read and agreed to the published version of the manuscript.

Funding

This study was partly funded by a PhD scholarship from AUIP-PAEDEX (Brazil). To the Asociación Universitaria Iberoamericana de posgraduación (AUIP) for the scholarship “Programa de Apoyo a Estudiantes de Doctorado del Extranjero (PAEDEX)”, to carry out the PhD program in Ciências Florestais at the Faculdade de Ciências Agronômicas, Universidade Estadual Paulista, Botucatu, San Pablo, Brazil. Additional funding was provided by the University of the Republic (UDELAR), in Uruguay. This work was supported in part by the program Proteção Florestal (PROTEF) from the Instituto de Pesquisas e Estudos Florestais (IPEF)”, Piracicaba, San Pablo, Brazil.

Data availability

Code availability

Is not applicable

Declarations Ethics approval

Not applicable

Conflicts of interest

All authors have read and don't present a conflict of interest.

References

1. Akhtar MS, Patankar NV, Gaur A (2012) Observations on the biology and male of eucalyptus gall wasp *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae). Indian J Entomol 74:173–175
2. Ankita G, Poorani J (2009) Taxonomic studies on a collection of Chalcidoidea (Hymenoptera) from India with new distribution records. J Threatened Taxa 1:300–304

3. Aquino DA, Botto EN, Loíacono MS, Pathauer P (2011) Avispa de la agalla del eucalipto, *Leptocybe invasa* Fischer & La Salle (Hymenoptera: Eulophidae: Tetrastichinae), en Argentina. *Revista de Investigación Agropecuaria (RIA)*, 37, 2, 159–164
4. Aquino et al (2019) First record of males of the invasive eucalyptus pest species *Leptocybe invasa* Fisher & LaSalle, 2004 (Hymenoptera: Eulophidae: Tetrastichinae) from South America. *Bonn zoological Bull* 68(2):205–207
5. Benítez-Dias EE, Costa VA, de Moraes GJ, Godziewsky D (2014) First record of *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) and *Rhombacus eucalypti* Ghosh & Chakrabarti (Acari: Eriophyidae) from Paraguay. *Boletín del Museo Nacional de Historia Natural de Paraguay*. 18(1): 129–132
6. Chen HY, Yao JM, Xu ZF (2009) First description of the male of *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) from China. *J Environ Entomol* 31:285–287 (in Chinese with English abstract)
7. Costa VA, Berti Filho E, Wilcken CF, Stape JL, LaSalle J, Teixeira LD (2008) *Eucalyptus* gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae) in Brazil. New forest pest reaches the new world. *Revista Agricultura* 83:136–139
8. Csóka G, Stone GN, Melika G (2017) Non-native gall-inducing insects on forest trees: a global review. *Biol Invasions* 19:3161–3181
9. De Souza AR (2016) Aspectos biológicos de *Leptocybe invasa* (Hymenoptera: Eulophidae) e de seu parasitoide *Selitrichodes neseri* (Hymenoptera: Eulophidae) e levantamento de vespas galhadoras em florestas de eucalipto na Austrália. PhD Thesis. Faculdade de Ciências Agrônômicas, UNESP, Campus de Botucatu. San Pablo, Brazil. 75 pp
10. DIEA-MGAP (División estadísticas agropecuarias-Ministerio de la Ganadería, Agricultura y Pesca) (2024) Anuario estadístico 2024. Accessed on Nov 09, 2025. Online access in: <https://descargas.mgap.gub.uy/DIEA/Anuarios/Anuario2024/Anuario2024/%20ANUARIO2024.pdf>
11. Dittrich-Schröder G, Hoareau TB, Hurley BP, Wingfield MJ, Lawson S, Nahrung HF, Slippers B (2018) Population genetic analyses of complex global insect invasions in managed landscapes: a *Leptocybe invasa* (Hymenoptera) case study. *Biol Invasions* 20:2395–2420
12. Doğanlar M (2005) Occurrence of *Lectocybe invasa* Fisher & La Salle, 2004 (Hymenoptera: Chalcidoidea) on *Eucalyptus camaldulensis* in Turkey, with a description of the male sex. *Zoology in the Middle East*. 35:1, 112–114
13. FAO (2024) El estado de los bosques del mundo. Innovaciones en el sector forestal para lograr un futuro más sostenible. Accessed on Nov 09, 2025. Online access in: <https://openknowledge.fao.org/server/api/core/bitstreams/542dc735-5ab6-41e0-9ea6-1e492ee4afda/content/cd1211es.html#gsc.tab=0>
14. Felsenstein J (1976) The evolutionary advantage of recombination. *Genetics* 78:737–756
15. Garnas JR, Auger-Rozenberg MA, Roques A, Bertelsmeier C, Wingfield MJ, Saccaggi DL, Roy HE, Slippers B (2016) Complex patterns of global spread in invasive insects: eco-evolutionary and

- management consequences. *Biol Invasions* 18:935–952. 10.1007/s10530-016-1082-9
16. Gibson IAS et al (1980) The adoption of agricultural practices for the development of heritable resistance to pests and pathogens in forest crops. In: editors
 17. Gualtieri L, Nugnes F, Nappo AG, Gebiola M, Bernardo U (2017) Life inside a gall: closeness does not favour horizontal transmission of *Rickettsia* between a gall wasp and its parasitoid. *FEMS Microbiol Ecol* 93:1–11
 18. Heimpel GE, de Boer JG (2008) Sex determination in the Hymenoptera. *Ann Rev Entomol* 53:209–230. 10.1146/annurev.ento.53.103106.093441
 19. Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. *Biol Invasions* 18:921–933
 20. Jorge C (2019) Ecologia de *Leptocybe invasa* (Hymenoptera: Eulophidae) e seus parasitoides e simbiontes em *Eucalyptus*. PhD Thesis. Faculdade de Ciências Agronômicas, Unesp, Botucatu, SP, Brasil. 160 pp
 21. Jorge C, Martinez G, Gomez D, Bollazzi M (2016) First record of the eucalypt gall-wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) from Uruguay. *Bosque (Valdivia)* 37:631–636
 22. Jorge C, Molina P (2020) Early detection and symptoms of *Leptocybe invasa* Fisher & La Salle, 2004 (Hymenoptera: Eulophidae) in *Eucalyptus* (Myrtaceae) nurseries. *Boletín de la Sociedad Zoológica del Uruguay* 29:132–140
 23. Kumari NK, Kulkarni H, Vastrad AS, Basavana GK (2010) Biology of eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae). *Karnataka J Agricultural Sci* 23:211–212
 24. Le NH, Nahrung HF, Griffiths M, Lawson SA (2018) Invasive *Leptocybe* spp. and their natural enemies: Global movement of an insect fauna on eucalypts. *Biol Control* 125:7–14
 25. Liang YP, Li JY, Wen XJ, Li YX (2010) Observation on the male ratio of *Leptocybe invasa* adult. *For Pest Disease* 29:21–22 (in Chinese with English abstract)
 26. Mendel Z, Protasov A, Fisher N, La Salle J (2004) Taxonomy and biology of *Leptocybe invasa* gen. & sp. n. (Hymenoptera: Eulophidae), an invasive gall inducer on *Eucalyptus*. *Australian Journal Entomology* 43:101–113
 27. Mendel Z, Protasov A, La Salle J, Blumberg D, Brand D, Branco M (2017) Classical biological control of two eucalyptus gall wasps; main outcome and conclusions. *Biol Control* 105:66–78
 28. Meurisse N, Rassati D, Hurley BP et al (2019) Common pathways by which non-native forest insects move internationally and domestically. *J Pest Sci* 92:13–27
 29. Misevic D, Ofria C, Lenski RE (2006) Sexual reproduction reshapes the genetic architecture of digital organisms. *Proceedings of the Royal Society B*. 273: 457–464
 30. Mota TA, Souza AR, Teixeira DL, Carvalho VR, Ribeiro MF, Hönnebeck J, Zanuncio JC, Wilcken CF (2025) *Leptocybe invasa* males and the parasitoid *Quadrastichus mendeli* (Hym.: Eulophidae): First report in Paraguay. *Brazilian Journal of Biology*. 85: e296582

31. Nadel RL, Slippers B (2011) *Leptocybe invasa*, the blue gum chalcid wasp. ICFR, South Africa. In: <http://www.forestry.co.za/uploads/File/home/notices/2011/ICFR%20IS01-2011gallwasp.pdf>. Accessed 15 Jan 2025
32. Nugnes F, Gebiola M, Monti MM, Gualtieri L, Giorgini M, Wang J, Bernardo U (2015) Genetic Diversity of the Invasive Gall Wasp *Leptocybe invasa* (Hymenoptera: Eulophidae) and of its *Rickettsia* Endosymbiont, and Associated Sex-Ratio Differences. PLoS ONE 10:1–20
33. Otieno BA, Nahrung HF, Steinbauer MJ (2019) Where Did You Come From? Where Did You Go? Investigating the origin of invasive *Leptocybe* species using distribution modelling. Forests 10(2):115. 10.3390/f10020115
34. Paine TD, Steinbauer MJ, Lawson SA (2011) Native and Exotic Pests of *Eucalyptus*: A Worldwide Perspective. Ann Rev Entomol 56:181–201
35. Rodas Peláez CA, Wingfield MJ (2021) Important insect pests and diseases of *Pinus* and *Eucalyptus* in Colombia. Smurfit Kappa. 180 p
36. Roques A, Copeland RS, Soldati L, Denux O, Auger-Rozenberg MA (2016) *Megastigmus* seed chalcids (Hymenoptera, Torymidae) radiated much more on Angiosperms than previously considered. I-Description of 8 new species from Kenya, with a key to the females of Eastern and Southern África. ZooKeys 585:51–124
37. Saavedra MC, Withers TM, Holwell GI (2015) Susceptibility of four *Eucalyptus* host species for the development of *Thaumastocoris peregrinus* Carpintero and Dellapé (Hemiptera: Thaumastocoridae). For Ecol Manag 336:210–216
38. SAG (Servicio Agrícola y Ganadero) (2014) *Leptocybe invasa* Fischer & LaSalle (Hymenoptera: Eulophidae) Microavispa formadora de agallas en eucalipto. Servicio Agrícola y Ganadero de Chile. In: <https://www.sag.gob.cl/ambitos-de-accion/microavispa-formadora-de-agallas-en-eucalipto-leptocybe-invasa-fischer-lasalle-hymenoptera-eulophidae>
39. Sangtongpraow B, Charernsom K, Siripatanadilok S (2011) Longevity, fecundity and development time of *Eucalyptus* gall wasp, *Leptocybe invasa* Fisher and La Salle (Hymenoptera: Eulophidae) in Kanchanaburi province, Thailand. Thai J Agric Sci 44:155–163
40. Stone G, Schonrogge K (2003) The adaptative significance of insect gall morphology. Trends Ecol Evol 18:512–522
41. Stouthamer R, Russell JE, Vavre F, Nunney L (2010) Intragenomic conflict in populations infected by Parthenogenesis Inducing Wolbachia ends with irreversible loss of sexual reproduction. BMC Evolutionary Biology, 10, 229. Doi: <http://www.biomedcentral.com/1471-2148/10/229>
42. Thu PQ, Bell B, Burgess TI (2009) Susceptibility of 18 eucalypt species to the gall wasp *Leptocybe invasa* in the nursery and young plantations in Vietnam. Sci Asia 35:113–117
43. Tung GS, LaSalle J (2010) Pest Alert a Newly Discovered Invasion of Gall forming Wasps, *Leptocybe invasa* (Fisher & LaSalle), on *Eucalyptus* Trees in Taiwan. Formosan Entomology, 30, 241–245
44. Udagedara U, Karunaratne W (2014) Biology, damage and parasitoids of the *Eucalyptus* gall wasp, *Leptocybe invasa* (Hymenoptera: Eulophidae), infesting *Eucalyptus camaldulensis* (Myrtaceae) in

- Maragamuwa plantation, Sri Lanka. Int Journal Trop Insect Science 34:179–189
45. Vershinina AO, Kuznetsov VG (2016) Parthenogenesis in Hexapoda: Entognatha and non-holometabolous insects. J Zoological Syst Evolutionary Res 54:257–268
 46. Wilcken CF, Zaché B, Masson MV, Pereira RA, Barbosa LR, Zanuncio JC (2015a) A vespa-da-galha-do-eucalipto, *Leptocybe invasa* Fisher & La Salle. In: Vilela EF, Zucchi RA (eds) Pragas Introduzidas no Brasil. Insetos e ácaros. Fealq, Em, pp 835–844
 47. Wilcken CF, Firmino-Winckler DC, Pogetto D, Dias MHFA, Lima TKR, de Sá ACV. L.A.N., Ferreira-Filho PJ (2015b) Psilídeo-de-concha-do-eucalipto, *Glycaspis brimblecombei* Moore. Em: Vilela, E.F., Zucchi, R.A. (eds) Pragas Introduzidas no Brasil. Insetos e ácaros. Fealq, Piracicaba, pp 883–897
 48. Wingfield MJ, Slippers B, Hurley BP, Coutinho TA, Wingfield BD, Roux J (2008) *Eucalypt* pests and diseases: Growing threats to plantation productivity. South Forests 70:139–144
 49. Zheng XL, Yang ZD, Li J, Xian ZH, Yang J, Liu JY, Su S, Wang XL, Lu W (2014a) Rapid identification of both sexes of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae: Tetrastichinae): a morphological perspective. Afr Entomol 22(3):643–650
 50. Zheng XL, Li J, Yang ZD, Xian ZH, Wei JG, Lei CL, Wang XP, Lu W (2014b) A review of invasive biology, prevalence and management of *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae). Afr Entomol 22:68–79. <http://dx.doi.org/10.4001/003.022.0133>
 51. Zheng X, Huang Z, Li J, Yang Z, Lu W (2017) Reproductive Biology of *Leptocybe invasa* Fisher & LaSalle (Hymenoptera: Eulophidae). Neotrop Entomol 47(1):19–25. 10.1007/s13744-017-0502-6
 52. Zheng X, Lin K, Huang Z, Li J, Yang Z, Yang X, Lu W (2018) Offspring sex ratio and reproductive tactics of *Leptocybe invasa* (Hymenoptera: Eulophidae): Testing the effect of environmental characteristics. Int J Trop Insect Sci 38:394–399. 10.1017/S1742758418000127

Figures

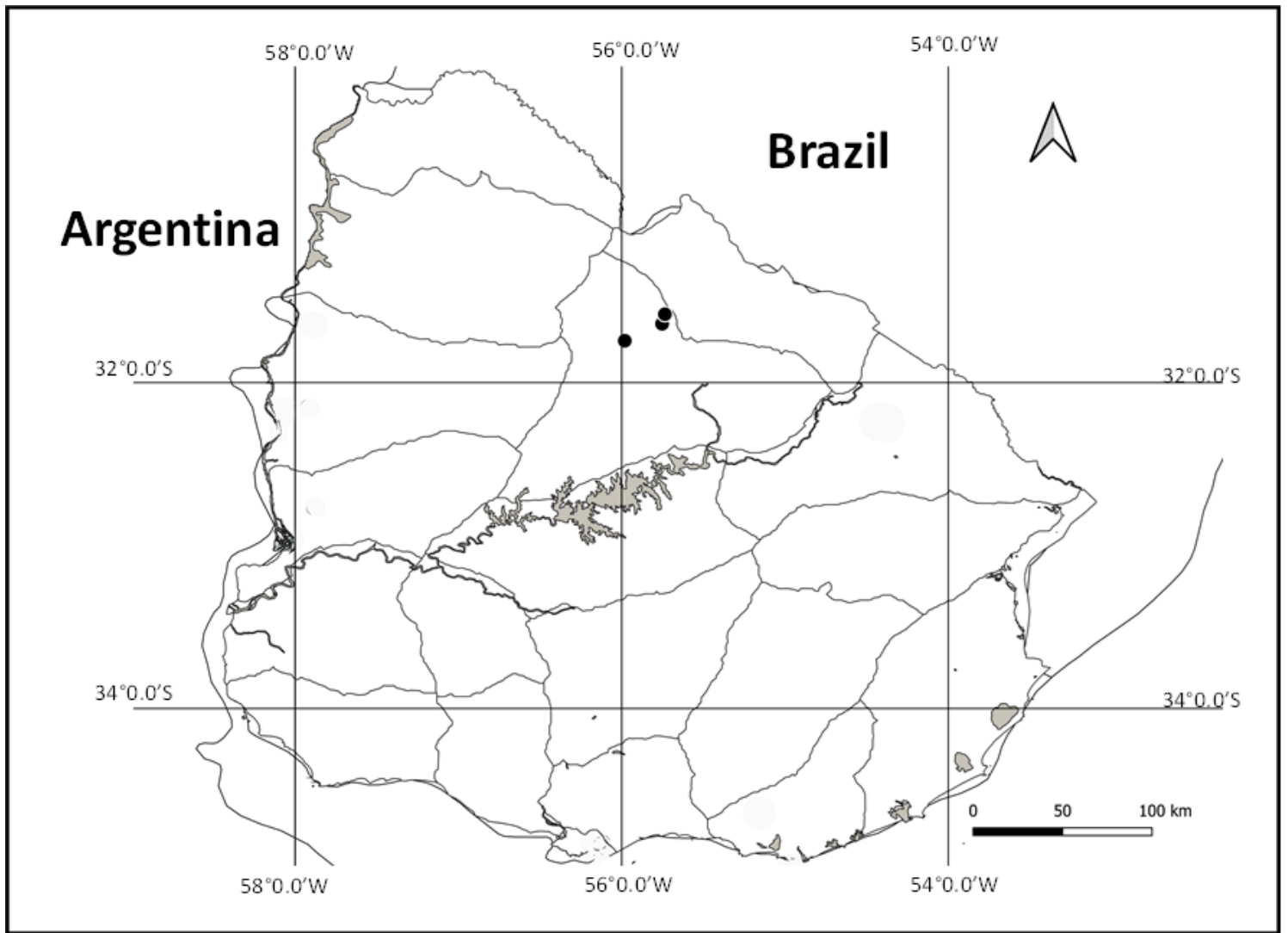


Figure 1

Sites where *L. invasa* males emerged from the collected galls during the field surveys. Black dots.

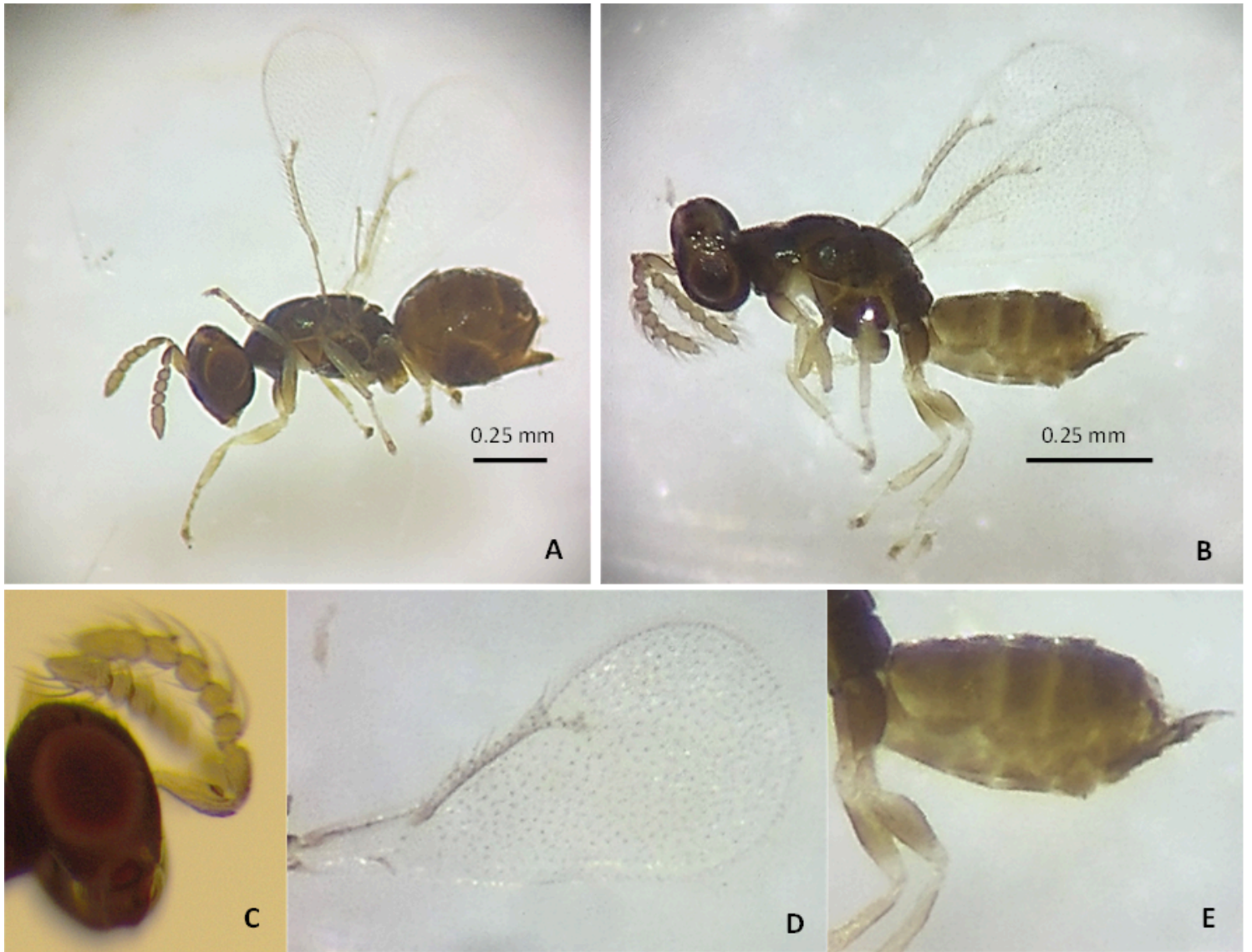


Figure 2

A. *Leptocybe invasa* adults from Uruguay. **A.** female. **B-E.** male. **A-B.** Lateral habitus, **C.** Antennae, **D.** Wing, **E.** Abdomen, and aedeagus details.