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Human-mediated plant dispersal changes insect distributions with important evolutionary implications

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Abstract

Human introductions of plant species often lead to secondary invasions by alien insects or range expansions by native ones. For instance, native insects may adopt introduced plants that are closely related to their native host plants. *Leptocoris* soapberry bugs feeding on plants in the Soapberry family (Sapindaceae) provide prime examples of such host shifts. In Australia and South Africa, the introduction of alien sapinds species, as well as human-mediated changes in the distributions of native sapinds, have the potential to impact the ecology and evolutionary dynamics of native soapberry bugs. We provide observations indicating that in both countries the ranges of some native *Leptocoris* species have expanded vastly due to the human-mediated movement and introduction of native and alien sapind species, respectively. In Australia, native *L. rufomarginatus* has established in the Sydney region where native host species have been introduced and naturalised well outside their historical ranges (i.e., extralimital species) and introduced alien *L. vicinus* was found localised at its initial introduction site in Darwin. In South Africa, native *L. mutilatus* now occurs ~1000km beyond previous records, feeding on the invasive balloon vine *Cardiospermum grandiflorum* and the alien tree *Alectryon connatus.* We provide evidence for differentiation in the proboscis length of *L. mutilatus* insects feeding on different alien, invasive and native host plants. In Australia, we successfully hybridised and backcrossed native *L. tagalicus* with alien *L. vicinus* under laboratory conditions, providing the first report of interspecific hybridisation for the genus. The high eco-evolutionary experience shared between soapberry bugs and their host plants suggest that further changes in these insects' distributions and adaptive responses to novel host plants are likely to occur. Taken together, our results demonstrate how human-mediated plant dispersal can impact on the ecology, distribution and evolution of insects.

Keywords: Eco-evolutionary experience, hybridisation, host shifts, invasive alien species, rapid evolution, range shifts, soapberry bugs

Introduction

Human-assisted dispersal of species over vast distances is a key feature of the Anthropocene, often resulting in the establishment of naturalised or invasive populations (Mack and Lonsdale, 2001). Biological invasions have numerous ecological and evolutionary impacts on native biodiversity (Mooney and Cleland, 2001, Kumar Rai and Singh, 2020). As hosts for insects, invasive plants may also facilitate secondary insect invasions (Bonnamour et al., 2023, Bertelsmeier et al., 2024), either directly through the unintentional translocation of insects on imported plants (Kenis et al., 2007, Liebhold et al., 2012, Meurisse et al., 2019, Smith et al., 2007) or indirectly, such as when they act as new resources for both native and alien insects (Dang et al., 2022; Mally et al., 2021; Morales and Aizen, 2002). Native insects may undergo range expansions (i.e., extralimital spread) when they encounter invasive plants closely related to their natural hosts, since many insects are specialised to use congeneric or confamilial plants (Hurley et al., 2016; Mally et al., 2021; Strauss et al., 2006). These evolutionarily familiar host shifts represent high eco-evolutionary experience (EEE), arising from pre-adaptations shaped by past biotic interactions (Le Roux, 2021; Saul et al., 2013; Saul and Jeschke, 2015)

The role of EEE in facilitating secondary insect invasions, or range expansions of native insects, is elegantly illustrated by soapberry bugs, a group of hemipterans of the genera *Boisea*, *Jadera*, and *Leptocoris* (Rhopalidae: Serinethinae). These insects are specialised seed predators of soapberry plants (Sapindaceae; Carroll and Loye, 2012). The co-introduction and spread of alien soapberry bugs and sapinds as well as range expansions by native soapberry bugs adopting alien Sapindaceae as new host plants, have been noted (Carroll and Loye, 2012, Faúndez et al., 2020, Tsai et al., 2013). For example, *L. vicinus* was likely accidently co-introduced with the ornamental tree *Schleichera oleosa* into Australia, from south-east Asia (Carroll et al., 2005b).

Australia is home to four native soapberry bugs: *L. isolatus*, *L. mitellatus*, *L. rufomarginatus*, and *L. tagalicus* (the latter has two subspecies, subsp. *vulgaris* and subsp. *tagalicus*) (Carroll et al., 2005b). Native *Alectryon* species constitute the highest diversity (n = 6) of known native host plants of soapberry bugs in the country and are utilised by three of the four *Leptocoris* species: *L. mitellatus*, *L. rufomarginatus*, and *L. tagalicus* (Carroll and Loye, 2012, Carroll et al., 2005b). In

eastern coastal Australia, *A. tomentosus* is a particularly important host for all three of these soapberry bug species. This medium-sized tree is found in a variety of coastal rainforest habitats from Cape York in northern Queensland (Qld) and southwards to the Hunter River in New South Wales (NSW) (Floyd, 2008). This tree has also been planted further south as an ornamental, particularly in the greater-Sydney region, where it has occasionally naturalised, primarily north of Sydney Harbour (Randall, 2001). Other native Australian *Alectryon* species, such as *A. coriaceous*, have also been planted as ornamental trees outside of their historical ranges.

Invasive Sapindaceae species have also impacted the distribution, ecology, and evolutionary dynamics of soapberry bugs in Australia. For example, genetic analysis indicated the two subspecies of *L. tagalicus* historically colonised the invasive balloon vine *Cardiospermum halicacabum* in the Northern Territory (NT) and hybridised to establish a highly differentiated biotype on this new host plant (Andres et al., 2013). Another balloon vine species, *C. grandiflorum,* has invaded large areas along Australia's east coast. This very large-fruited vine was colonised by *L. tagalicus* subsp. *tagalicus* and museum specimens of the insect collected between the 1920s and 2000 revealed that it has evolved longer proboscides, likely in response to the larger size of *C. grandiflorum* fruits compared to those of the native host plants utilised by the insect (Carroll et al., 2005a). The longer proboscides have been retained in contemporary *L. tagalicus* populations on invasive balloon vines (Le Roux et al., 2025a).

The human-mediated introduction, naturalisation, and spread of both alien and native sapinds may have other ecological and evolutionary consequences for soapberry bugs in Australia, and possibly elsewhere. For example, of the three native soapberry bug species feeding on *Alectryon* species in Australia, *L. rufomarginatus* is the most range-restricted and host-limited species (Carroll et al., 2005b). On the basis of historical museum records, the native range of this species is posited to extend from the northern NT through eastern Qld and into northeastern NSW (Carroll et al., 2005b). It is possible that this species has expanded its distribution southwards where its *Alectryon* hosts have been introduced and became naturalised. Similarly, the range limits of *L. tagalicus* have changed dramatically throughout Australia because of balloon vine invasion (Carroll et al., 2005a). These distributional changes may also create opportunities for different *Leptocoris* species to come into contact in southern

NSW. For example, *L. rufomarginatus* and *L. tagalicus* have been observed on the same host plants in regions where their distributions overlap (Carroll et al., 2005b). Where host plant availability and conspecific abundance is low at the edges of their distributional ranges, there is an increased likelihood of contact and possible hybridisation between these two soapberry bug species. This is particularly plausible given the geographic extent of invasive and extralimital host plants that can support both species (Bridle and Vines, 2007). Similarly, the close geographic proximity of invasive *C. halicacabum*, a known host of *L. vicinus* (Li et al., 2025, Carroll and Loye, 2012), the planting of *S. oleosa* in the NT suggests that contact between native *L. tagalicus* and alien *L. vicinus* may lead to hybridisation.

Host shifts by soapberry bugs, followed by evolutionary responses in the insects, are likely replicated in other parts of the world. For instance, invasive balloon vines in South Africa may also create opportunities for the expansion of native *Leptocoris* species. Both *C. grandiflorum* and *C. halicacabum* were introduced into the country over 100 years ago (Gildenhuys et al., 2013) and phylogenetic and morphological analyses have shown that native *L. mutilatus* in association with these two hosts are genetically and morphologically distinct (Foster et al., 2019). *Cardiospermum grandiflorum* is more widely distributed in South Africa than *C. halicacabum*, with its range extending far beyond the historical range of *L. mutilatus* and its primary native host plant, *Cardiospermum corindum*. It is therefore possible that *L. mutilatus* has undergone a range expansion in South Africa following the invasion by *C. grandiflorum*.

Here we aimed to assess whether human-mediated introductions of native and alien sapindaceous host plants have been accompanied by range expansions of *Leptocoris* soapberry bugs in Australia and South Africa. In Australia, we also aimed to assess whether hybridisation between alien, native extra-limital, and native *Leptocoris* species is possible. We hypothesised that range expansions of *Leptocoris* species are occurring in both countries following human-mediated dispersal of host plants, with the potential to break down historical geographic barriers between them. We predicted that *L. rufomarginatus* will be present on *Alectryon* in southern NSW where *Alectryon* species have been planted or naturalised outside of their more northerly historical ranges, that *L. vicinus* will still be present on *S. oleosa* in Darwin, in the NT (over 60 years since first discovered). We also hypothesised that some

native and alien *Leptocoris* species in Australia will be able to hybridise when occurring on the same host plants in the same areas. In South Africa, we aimed to determine whether *L. mutilatus* insects feeding on different alien, invasive and native host plants differ in proboscis length, a key trait for effective feeding on many sapindaceous seeds. We hypothesised that insects collected on different host plants in South Africa will have distinct proboscis lengths. We also predicted that *L. mutilatus* will occur well outside of its historical native range in this country.

Materials and Methods

Field collections

Field collections of *Leptocoris* insects in Australia were made at six locations in NSW and one location in the NT (Table 1). In NSW, insects were collected from *Alectryon tomentosus* at four locations and *A. coriaceous* at two locations. Initial collections of *L. rufomarginatus* were from Macquarie University and Wingham Brush Nature Reserve (Table 1; see species identification below) during collections targeting *L. tagalicus*. These observations initiated further searches for this species at locations with potential host plant species beyond the previous known range limits of the insect. Collections of *L. vicinus* were made at the George Brown Darwin Botanic Gardens in Darwin. Further searches for *Leptocoris* species on likely introduced hosts (*Cardiospermum halicacabum* or *Koelreuteria elegans*) were conducted in areas around Darwin (up to 30 km away), however, none were present and we did not identify *L. vicinus* at any other location in the NT (insects on *C. halicacabum* were sampled at sites from Daly River Crossing to Kakadu National Park; these collections are not included as part of this study).

At each site we aimed to collect up to 15 insects, including nymphs. Adult insects were euthanised or collected when dead, and nymphs were raised to adulthood in the laboratory. Proboscis length, body length, and pronotum width were measured using digitised callipers (+/- 0.01mm). Euthanised insects were preserved in 90% ethanol and stored at -80°C. Prior to euthanasia, a subset of *L. rufomarginatus* individuals were used to start a captive colony for hybridisation experiments. A subset of *L. vicinus* nymphs was collected and raised to adulthood solely to start a captive colony. The *L. tagalicus* insects used in our hybridisation experiment originated from

a captive colony descending (2-3 generations) from wild insects from south-eastern Qld.

In South Africa, we collected *L. mutilatus* insects from 10 sites in parts of the insect's historical native range, in Kruger National Park. These insects were collected from either native *Cardiospermum corindum* or invasive *C. halicacabum.* Three extralimital sites were also identified, in the Western Cape province. Insects were collected from invasive *Cardiospermum grandiflorum* at two of these sites, and from a horticultural planting of the Australian native tree *Alectryon connatus* at the third. Where possible, up to 20 adult insects were collected from each site. Proboscis length, body length, and pronotum width were measured using digital callipers (+/- 0.01mm). We also quantified the wing morphology of each insect as short-winged (i.e. flightless) or long-winged (i.e. volant). Insects were euthanised and preserved in 90% ethanol and stored at -80°C.

Collections were made in Australia and South Africa under permits issued by the NSW Department of Planning, Industry and Environment (licence number: SL102654), South African National Parks (SANParks permit number: SS1156) and CapeNature (licence number: CN44-87-34332). No collection permit was required for the collection of alien *L. vicinus* in the NT (Peter Ross, Parks and Wildlife Commission, personal communication).

Averages and standard errors for all three body measurements were calculated using the *dplyr* R package (Wickham et al., 2023) in R version 4.4.0 (R Core Team, 2024).

Table 1. Details of sites where *Leptocoris* species were collected. Included is the host plant species that insects were collected on and its status at that location: native (naturally occurring), ornamental (planted at the location), alien (introduced outside of native range), naturalised (introduced outside of native range and forming self-sustaining populations), and invasive alien (naturalised, spreading, and causing ecological impacts).

Host species	Host status	Site name	Territory/State/ Province	Latitude	Longitude
Australia					
Alectryon coriaceous	Alien ornamental	Macquarie University	NSW	-33.77352	151.11648
Alectryon coriaceous	Alien ornamental	Manly	NSW	-33.79172	151.28359
Alectryon tomentosus	Native	Wingham Brush	NSW	-31.86981	152.37909
Alectryon tomentosus	Naturalised	Turramurra	NSW	-33.73358	151.12625
Alectryon tomentosus	Alien ornamental	Killara	NSW	-33.76215	151.15866
Alectryon tomentosus	Alien ornamental (Botanic Garden)	Royal Botanic Garden Sydney	NSW	-33.86219	151.21530
Schleichera oleosa	Alien ornamental (Botanic Garden)	George Brown Darwin Botanic Gardens	NT	-12.44575	130.83667
South Africa					
Alectryon connatus	Alien ornamental	Van Riebeeck St.	Western Cape	-33.93645	18.86981
Cardiospermum corindum	Native	Biyamiti 1	Mpumalanga	-25.26578	31.62481
Cardiospermum corindum	Native	Biyamiti 2	Mpumalanga	-25.28050	31.62162
Cardiospermum corindum	Native	Biyamiti 3	Mpumalanga	-25.28320	31.61943
Cardiospermum corindum	Native	Sabie 4	Mpumalanga	-24.99219	31.76673
Cardiospermum corindum	Native	Sabie 5	Mpumalanga	-25.06665	31.81411
Cardiospermum grandiflorum	Invasive alien	Kromrivier 1	Western Cape	-33.92645	18.86139
Cardiospermum grandiflorum	Invasive alien	Kromrivier 2	Western Cape	-33.89477	18.89477
Cardiospermum halicacabum	Invasive alien	Sabie 1	Mpumalanga	-24.98073	31.63994
Cardiospermum halicacabum	Invasive alien	Sabie 2	Mpumalanga	-24.96520	31.70211
Cardiospermum halicacabum	Invasive alien	Afsaal	Mpumalanga	-25.29520	31.53173
Cardiospermum halicacabum	Invasive alien	Skukuza	Mpumalanga	-24.99111	31.60166
Cardiospermum halicacabum	Invasive alien	Tshokwane Rd.	Mpumalanga	-25.01643	31.86846

Leptocoris species identification

All collected insects in Australia were identified to species level using a combination of overall visual appearance, features of genitalia, and morphometrics based on the descriptions provided by Gross (1960) and Carroll et al. (2005b). *Leptocoris vicinus* is distinct from all other *Leptocoris* species present in Australia having dark and V-shaped coloration around the scutellum, although the intensity of this can vary among individuals. Male genitalia of this species are also distinctive with a dorsally smooth parandria and lacking a prominent groove (Gross, 1960). *Leptocoris rufomarginatus* is substantially larger than all other species present in Australia, with distinctive (and variable) iridescent green wing patches and bold lateral striping on the abdomen (Carroll et al., 2005b).

Insects collected in South Africa were identified to species level using a combination of visual appearance, features of genitalia, and morphometrics based on the descriptions of Göllner-Scheiding (2008). Both *L. mutilatus* and the superficially similar *L. hexophthalmus* subsp. *hexophthalmus* are present in South Africa. *Leptocoris hexophthalmus* is less red in appearance and has black and brown undertones absent in *L. mutilatus*. It also lacks a longitudinal ridge that passes through the centre of the pronotum (Göllner-Scheiding, 1980).

Analysis of Australia host plant abundance, distribution and utilisation by soapberry bugs

To establish a list of known host plant species utilised by *L. rufomarginatus*, *L. tagalicus* and *L. vicinus* in Australia, we used a combination of information available from Carroll et al. (2005b), Carroll and Loye (2012), the soapberrybugs.org website (Carroll et al., 2014), and personal observations. For *L. vicinus,* which in Australia has only been found feeding on *S. oleosa*, we included hosts known to be utilised by the species in its native range that are also present as introduced alien species in Australia. While we successfully raised *L. vicinus* in the laboratory on *C. grandiflorum* seeds, this was not included as a host plant as it has not been previously recorded as a host for the insect. Plants used as nectar sources (e.g., species in the families Proteaceae, Myrtaceae, Fabaceae) were excluded from the host list.

To determine abundance and distribution of host plant species used by the three soapberry bugs in Australia, we collected occurrence records from the Atlas of Living Australia (ALA) (Belbin et al., 2021). Records were downloaded and filtered using the *galah* (Westgate et al., 2025) and *dplyr* (Wickham et al., 2023) R packages. To exclude overseas occurrence records of host plants, we restricted data points within a longitudinal range of 110 to 155 and a latitudinal range of -45 to -10 degrees. For duplicate geographic records, the oldest record was retained. All records without an associated date were excluded. Summary statistics were calculated using the *dplyr* R package.

Hosts range maps were created using the R packages *ggplot2* (Wickham, 2016), *ggspatial* (Dunnington, 2023), *Ozmaps* (Sumner, 2021), and *patchwork* (Pedersen, 2024). The R package *SF* (Pebesma, 2018, Pebesma and Bivand, 2023) was used to reproject map shape files to the 4326-coordinate reference system used by ALA and transform both geographical data and host records to polygons.

Analysis of South African L. mutilatus data

After confirming normality and homogeneity of variance in our data, we used a two-way ANOVA to test for differences in proboscis length of *L. mutilatus* insects from different host plant species, between insect sexes, and their interaction. Significant means were separated using Tukey HSD post hoc analyses. These analyses were

performed in the R statistical environment (R Core Team 2023). We compared the frequencies of short- and long-winged *L. mutilatus* morphs between insects from the extralimital range (i.e., Western Cape Province) and native areas (i.e., Kruger National Park), using a chi-square test of independence with Yates' continuity correction.

Hybridisation experiments

To assess whether *L. tagalicus, L. rufomarginatus* and *L. vicinus* are able to hybridise, we performed laboratory breeding experiments. Initial first-generation (G1) insect pairs consisted of reciprocal male and female pairings of *L. tagalicus* and *L. vicinus*, *L. rufomarginatus* and *L. tagalicus*, and *L. rufomarginatus* and *L. vicinus*. Each combination was replicated four times.

Prior to adult pairing, we isolated individual G1 5th instars in ventilated plastic containers and allowed them to moult to adulthood, ensuring that the paired insects were virgins. Paired insects were kept in a temperature-controlled glasshouse, covered internally and externally by shade cloth, at Macquarie University's Plant Growth Facility (6:00-10:30 at 26°C, 10:30-16:00 at 28°C, 16:00-18:00 at 26°C, and 18:00-06:00 at 20°C). Pairing of insects was completed in a randomised order. *Leptocoris tagalicus* and *L. vicinus* pairs were given access to a small piece of egg carton for shelter, a water vial, and two *C. grandiflorum* seeds. Pairs involving *L. rufomarginatus* were fed 50% *C. grandiflorum* seed and 50% *Alectryon tomentosus* as this species is not known to feed on *C. grandiflorum*. Each pair was given one to two fresh seeds and fresh water on a weekly basis. Pairs were kept for up to four months or the lifetime of the female, if shorter. After this period, both adults were euthanised,preserved in 90% ethanol, and stored at -80°C. Once a week, eggs, where present, were transferred into a separate container with water and seed. For eggs that hatched, nymphs were removed into a separate "nymph" box where they were kept until they had reached 5th instar stage or when they had recently moulted into adults and were then isolated to be used for a second generation.

Only *L. tagalicus* and *L. vicinus* pairings produced offspring (see Results). To test whether these hybrid offspring were reproductively viable, we conducted second generation (G2) pairings. This experiment consisted of F_1 crosses and reciprocal male and female backcrosses to *L. tagalicus* or *L. vicinus*. Each cross type was replicated eight times under the same conditions as the G1 pairings.

Following the pairing of G2 adults, eggs were moved into a separate container on a weekly basis. Where possible, adults were replaced if they died early in the experiment. Feeding and water changes followed the same regime as with G1. We removed any hatchlings and placed them in a separate nymph container. We attempted to raise as many nymphs as possible to adulthood to collect five adults of each sex from each treatment combination, which were then euthanised and preserved as described for G1 for downstream genetic analyses. After four months, all pairs were terminated, and adults were euthanised and preserved.

DArT library preparation and sequencing

The head, thorax, and legs of 126 adult *Leptocoris* insects from the hybridisation experiments were transferred to 96-well plates. Where required, tissue from the abdomen was used instead. In these cases, we dissected out the stomach and reproductive organs. Samples were sent to Diversity Arrays Technology (DArT, Canberra, Australia) for DNA extraction and next generation sequencing.

DNA was extracted from tissue samples using the NucleoMag kit (MACHEREY-NAGEL). *PstI* and *HpaII* compatible adaptors with two different restriction enzyme overhangs (Sansaloni et al., 2011) were designed to include the Illumina flowcell attachment sequence, sequencing primer sequence and a “staggered”, variable length barcode region following Elshire et al. (2011). The reverse adaptor contained the flowcell attachment region and *HpaII* compatible overhang sequence. Only “mixed fragments” were effectively amplified in 30 rounds of PCR using the following PCR cycle: initial denaturation at 94°C for 1 min followed by 30 cycles of 94°C for 20 s, 58°C for 30 s, 72°C for 45 s and a final extension at 72°C for 7 min.

After PCR amplification, equimolar amounts of amplified product were bulked and subjected to 100 cycles of single read sequencing on the Illumina NovaSeq, NovaSeq X+ sequencer. Sequences generated from each lane were processed using proprietary DArT analytical pipelines. In the initial pipeline, poor quality sequences were removed, with more stringent filtering parameters applied to the barcode region compared to the rest of the sequence, ensuring reliable assignment of the sequences to specific samples (based on the “barcode split”). An average reproducibility score was produced for each locus by technical replication for ~20% of the samples through the entire DNA extraction and genotyping process.

Genetic analysis

The resulting SNP data was co-analysed with data for wild *L. tagalicus* and *L. vicinus* collections (unpublished data; Table S2). Additional quality control filtering was applied to the full SNP dataset using the *dartR* R package (Gruber et al., 2018, Mijangos et al., 2022). First, loci were excluded if they were monomorphic, were assigned a reproducibility score <0.98, did not meet the minimum read depth of 8 or had exceptionally high read depth that may indicate paralogy (> mean read depth + 3* standard deviation read depth). Next, we conducted iterative filtering for individual and locus call rates. To remove poor quality loci and individuals, we excluded loci with a call rate <0.5 and individuals with a call rate <0.3. We then increased these thresholds to a locus call rate 0.7 and individual call rate 0.6, avoiding high thresholds that may favour the detection of loci present in only one *Leptocoris* species. Loci that were no longer polymorphic after the removal of low-quality individuals were removed. To guard against false SNPs, loci with a minor allele count <3 were removed. In cases where more than one SNP position was recorded within a single read (i.e., physically linked), only a single SNP position was retained. Here, the most informative SNP was selected based on the average polymorphism information content. Lastly, loci were tested for deviations from Hardy-Weinberg equilibrium. This test included only wild reference populations in equal numbers from each species. Loci were excluded from the main dataset if they deviated from Hardy-Weinberg equilibrium in any population, after correction for multiple tests using the false discovery rate method ($q < 0.05$).

The resulting SNP dataset was used to examine the genetic relationship between samples via principal components analysis (PCA) in *dartR*. The number of probable population genetic clusters was inferred via sparse non-negative matrix factorisation (sNMF) in the *LEA* R package (Frichot and François, 2015).

Results

Field collections

We collected nine *Leptocoris vicinus* individuals (six males; two females; one nymph) in the NT that were measured and preserved for sequencing. A further 24 insects were collected and used to create a captive colony for later use in the hybridisation experiment and were not measured or included in the DNA sequencing analyses. In

NSW, we collected 40 *L. rufomarginatus* individuals (21 males; 19 females). Of these insects, three were collected from a single site within the natural distribution of host plants of this species (i.e., Hunter River; Table 1), while most individuals were collected from *Alectryon tomentosus* in areas south of this natural distribution, approximately 500km south of the species' previously published distribution. Notably, we also collected 17 individuals from two sites on *A. coriaceous*, a novel host record for this insect.

Leptocoris vicinus females had an average body length of 13.52 ± 0.42mm, proboscis length of 6.66 ± 0.20mm, and pronotum width of 3.38 ± 0.01mm, while males had an average body length of 9.56 ± 0.71mm, proboscis length of 6.01 ± 0.12mm, and pronotum width of 2.58 ± 0.13mm. *Leptocoris rufomarginatus* females at all sites had an average body length of 14.10 ± 0.26mm, proboscis length of 7.70 ± 0.07mm, and pronotum width of 4.03 ± 0.09mm, while males had an average body length of 13.08 ± 0.15mm, proboscis length of 7.29 ± 0.07mm, and pronotum width of 3.62 ± 0.05mm.

In South Africa, we collected a total of 169 *L. mutilatus* (81 males; 88 females) insects and a sole *L. hexophthalmus* subsp. *hexophthalmus* individual from the Western Cape province, and two *L. amictus* individuals from Kruger National Park. In the Western Cape province, 19 *L. mutilatus* individuals were collected from one site on an ornamental planting of alien *A. connatus,* while the *L. hexophthalmus* and all other *L. mutilatus* insects were collected on invasive *C. grandiflorum*.

Leptocoris mutilatus females across sites had an average body length of 13 ± 0.12mm, proboscis length of 6.17 ± 0.05mm, and pronotum width of 3.37 ± 0.04mm, while males had an average body length of 11.1 ± 0.1mm, proboscis length of 5.68 ± 0.04mm, and pronotum width of 2.89 ± 0.04mm.

A two-way ANOVA to evaluate the effects of host plant species and *L. mutilatus* sex on insect proboscis length found significant main effects for host plant ($F_{3,166}$ = 28.41, $p < 0.001$) and sex ($F_{1,166}$ = 52.07, $p < 0.001$), while their interaction was not significant ($F_{3,166}$ = 1.48, $p = 0.22$). Tukey's post hoc analyses showed that, irrespective of host plant, female insects always had longer proboscides than male insects. Further, insects collected from invasive *C. halicacabum* had significantly longer proboscides than those collected from the other host plant species, while those

collected from native *C. corindum* had longer proboscides than those collected from alien *A. connatus* and invasive *C. grandiflorum.* The proboscis lengths of insects collected from the latter two hosts did not differ significantly. Except for insects collected from *C. grandiflorum,* average proboscis length at sites generally increased as the average fruit size of host plants increased (Figure 1B).

The frequencies of short and long wing morphs of *L. mutilatus* differed significantly between extralimital (i.e., Western Cape province) and native (i.e., Kruger National Park) range sites ($\chi^2_1 = 87.98$, $p < 0.001$). Of the 33 insects collected from the Western Cape province, 97% were short-winged, and of the 136 collected in Kruger National Park, 12.5% were short-winged.

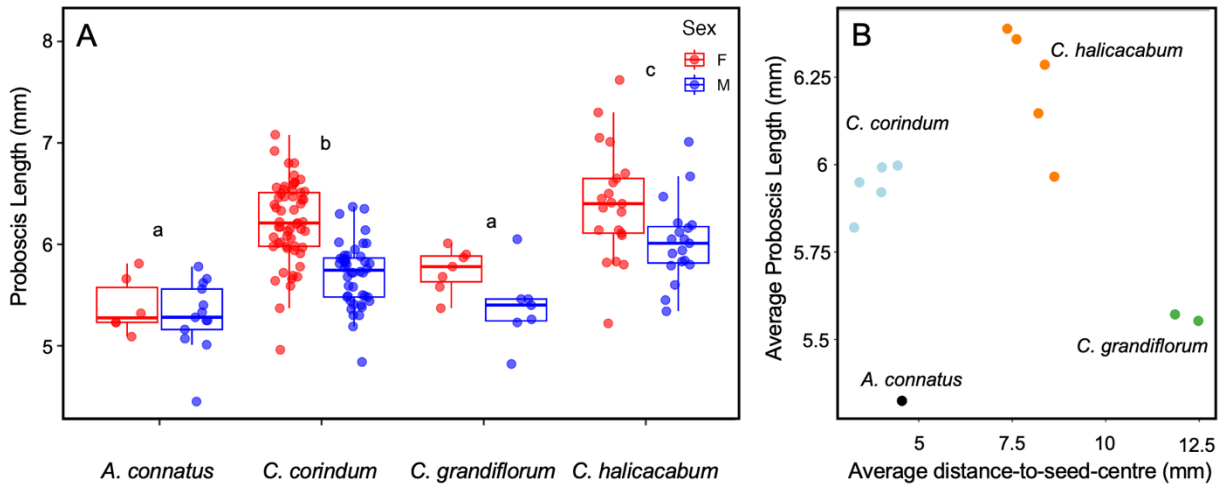


Figure 1. (A) The proboscis length of field-collected male and female *Leptocoris mutilatus* insects collected from the four different host plant species in South Africa, with significant differences between different host plant species indicated by different letters above boxplots ($p < 0.05$). (B) The average proboscis length of *L. mutilatus* insects collected at each site against the average distance to the seed centre for the host plant species they were collected from.

Host plant abundance, distribution and utilisation in Australia

In Australia, we identified a total of sixteen host plant species that are known to be utilised by *L. tagalicus*, seven by *L. rufomarginatus*, and four by *L. vicinus* (Table 2). *Leptocoris tagalicus* and *L. rufomarginatus* share seven host species (i.e. all the known host species utilised by *L. rufomarginatus*), while *L. vicinus* shared no hosts with *L. rufomarginatus* and three with *L. tagalicus*.

Our ALA search of occurrence records for these 17 plant species returned a total of 24,876 occurrence records. Most of these records were for native species (n =

22,395). *Cardiospermum grandiflorum* was the most recorded alien host species (n = 1,597) and had fewer records than only four of the native plant species (*Alectryon oleifolius* n = 7,569, *A. subcinereus* n = 2,561, *Atalaya hemiglauca* n = 3,856, *Jagera pseudohorus* n = 3,661; Table 2). Most records were from the eastern coastal region of Australia, where the greatest number of records of alien hosts were also recorded (Figure 2). Isolated observations for *C. grandiflorum* were also recorded around Perth (Western Australia), Adelaide (South Australia), and Cairns (far-north Qld). The second most recorded alien host species was *C. halicacabum* (n = 353), with records clustered around the tropical savannahs of the NT and the eastern coast of Qld, as well as around Sydney, NSW.

Table 2. Occurrence records of all known host plant species, including novel hosts, utilised by *L. rufomarginatus*, *L. tagalicus*, and *L. vicinus* in Australia. 'Host for' refers to which of the three *Leptocoris* species are known to feed on the seeds of the plant species within or outside of Australia.

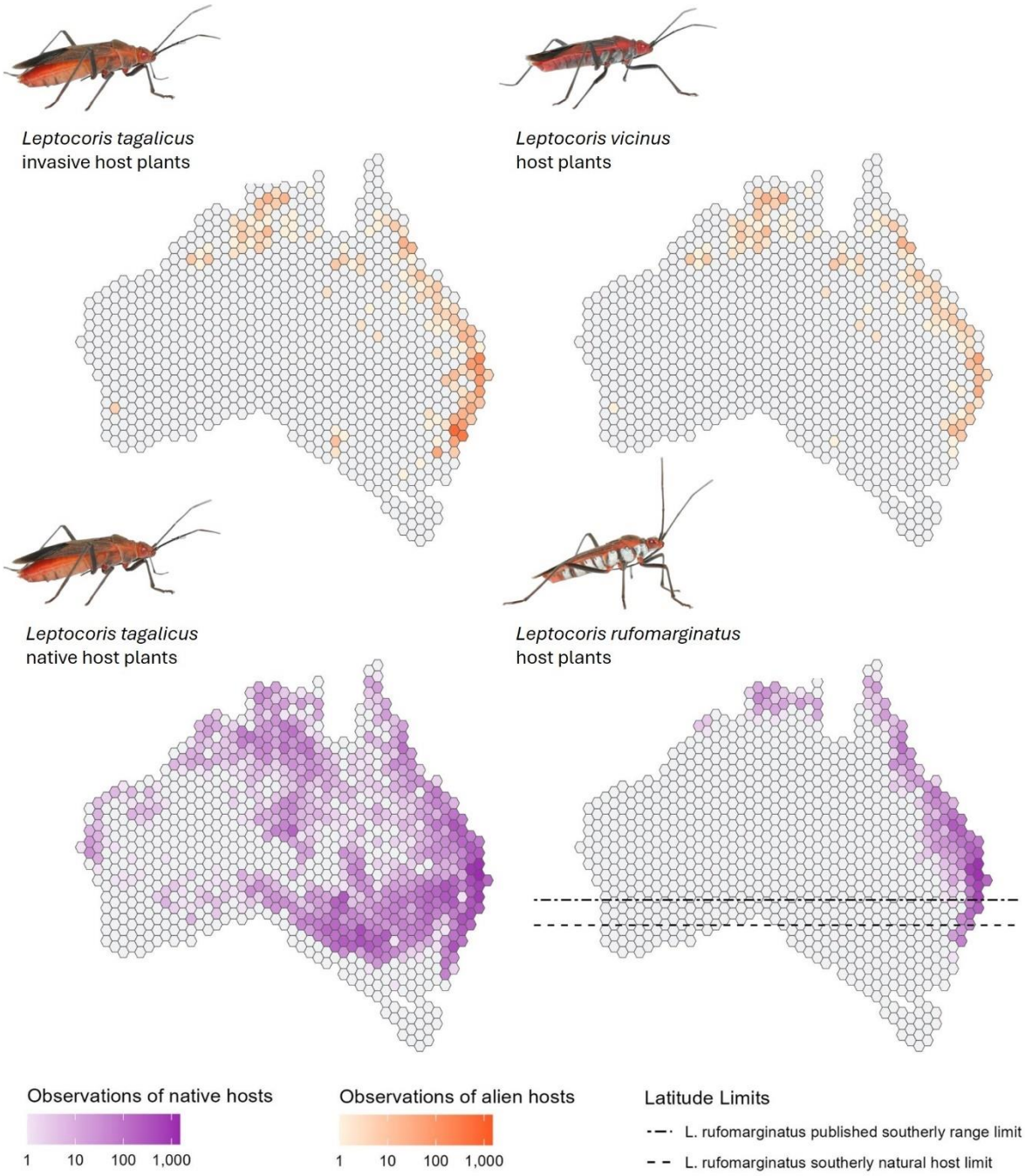
Host plant species	Number of plant records	Host for	Status in Australia
Alectryon connatus	636	*L. tagalicus* *L. rufomarginatus*	Native
Alectryon coriaceous	546	*L. tagalicus* *L. rufomarginatus*	Native; naturalised around Sydney, NSW
Alectryon diversifolius	532	*L. tagalicus* *L. rufomarginatus*	Native
Alectryon oleifolius	7569	*L. tagalicus*	Native
Alectryon subcinereus	2561	*L. tagalicus*	Native
Alectryon subdentatus	732	*L. tagalicus*	Native
Alectryon tomentosus	1121	*L. tagalicus* *L. rufomarginatus*	Native; Naturalised south of the Hunter River, NSW
Allophylus cobbe	299	*L. tagalicus* *L. rufomarginatus*	Native Native
Atalaya hemiglauca	3856	*L. tagalicus*	Native
Atalaya salicifolia	492	*L. tagalicus*	Native
Cardiospermum grandiflorum	1646	*L. tagalicus*	Invasive
Cardiospermum halicacabum	353	*L. tagalicus* *L. vicinus*†	Invasive
Elattostachys xylocarpa	688	*L. tagalicus* *L. rufomarginatus*	Native with few records outside of core range

Jagera pseudohorus	3661	*L. tagalicus* *L. rufomarginatus*	Native
Koelreuteria elegans	97	*L. tagalicus* *L. vicinus*†	Naturalised
Koelreuteria paniculata	81	*L. tagalicus*	Introduced; naturalised in some localities
Schleichera oleosa	4	*L. vicinus*	Introduced

† The insect has not been reported using this plant species as a host in Australia but is known to use it elsewhere (Carroll and Loye 2012).

ALA records of the four historically known native hosts of *L. rufomarginatus* present in NSW (i.e., *Alectryon diversifolius*, *A. tomentosus*, *Elattostachys xylocarpa,* and *Jagera pseudorhus*) and the novel host recorded here (*A. coriaceous*) included observations south of the Coffs Coast Region (~ -30.4 degrees latitude), which was the previously established southern limit of the insect (Carroll et al. 2005). Both *A. coriaceous* (n = 17) and *A. tomentosus* (58) have been recorded beyond the Hunter River (~ -32.7 degrees latitude), particularly in the northern suburbs of Sydney. *Jagera pseudorhus* (n = 10) and *Elattostachys xylocarpa* (7), on the other hand, had fewer occurrence

429 records in this part of Australia.



430

431

432 **Figure 2.** Tessellation maps of the density of records of native and alien host plant
433 species known to be utilised by the three focal *Leptocoris* soapberry bugs we studied
434 in Australia, retrieved from the Atlas of Living Australia.

435

436 *Hybridisation experiment*

In our staged breeding experiment, we witnessed the successful production of offspring in crosses between *L. vicinus* and *L. tagalicus*, as well as in both backcrosses. The performance of these offspring was generally poor, with several nymphs dying before reaching adulthood, and isolated adults dying prior to pairing for subsequenty crosses. While we did not count the exact number of males and females produced by each pair, from female *L. tagalicus* × male *L. vicinus* crosses, we only successfully obtained female offspring , while both male and female offspring were obtained from the reciprocal cross (see supplementary data). All F_1 × F_1 crosses produced eggs but no offspring (i.e. hatchlings). Pairings of *L. rufomarginatus* with both *L. vicinus* and *L. tagalicus* produced eggs but did not result in the production of hatchlings. No copulations were observed between *L. rufomarginatus* and the other two species, while copulations (or at least attempts) of *L. vicinus* and *L. tagalicus* crosses were regularly observed.

Genetic analysis

Quality control filtering resulted in a final dataset of 6,077 SNP loci and 71 insects for genetic analysis (Table S2). The PCA presented clear clustering of individuals according to their species and cross type (Figure 3). The first principal component explained 65.2 % of the variation and separated individuals according to species, with pure *L. tagalicus* (wild and captive) at one end and pure *L. vicinus* (wild and captive) at the other. Individuals produced in laboratory crosses (i.e. F_1 hybrids and backcrosses) were clustered between the two species clusters. We also assessed genetic admixture based on a genomic assignment test (Figure 4). When considering two genetic clusters (i.e, K = 2), individuals were broadly separated into pure *L. tagalicus* and pure *L. vicinus*, with F1 offspring and backcrossed individuals displaying substantial admixture at expected levels. Male F1 insects, all of which were from male *L. tagalicus* × female *L. vicinus* cross showed a higher proportion of assignment to *L. vicinus* than expected. The results for assignment to three genetic clusters (i.e., K = 3) corroborated our findings for K = 2. That is, F_1 individuals were assigned to a distinct cluster, in addition to the two clusters for pure *L. tagalicus*, pure *L. vicinus*, with admixture mostly observed in the backcrossed individuals (Fig S2).

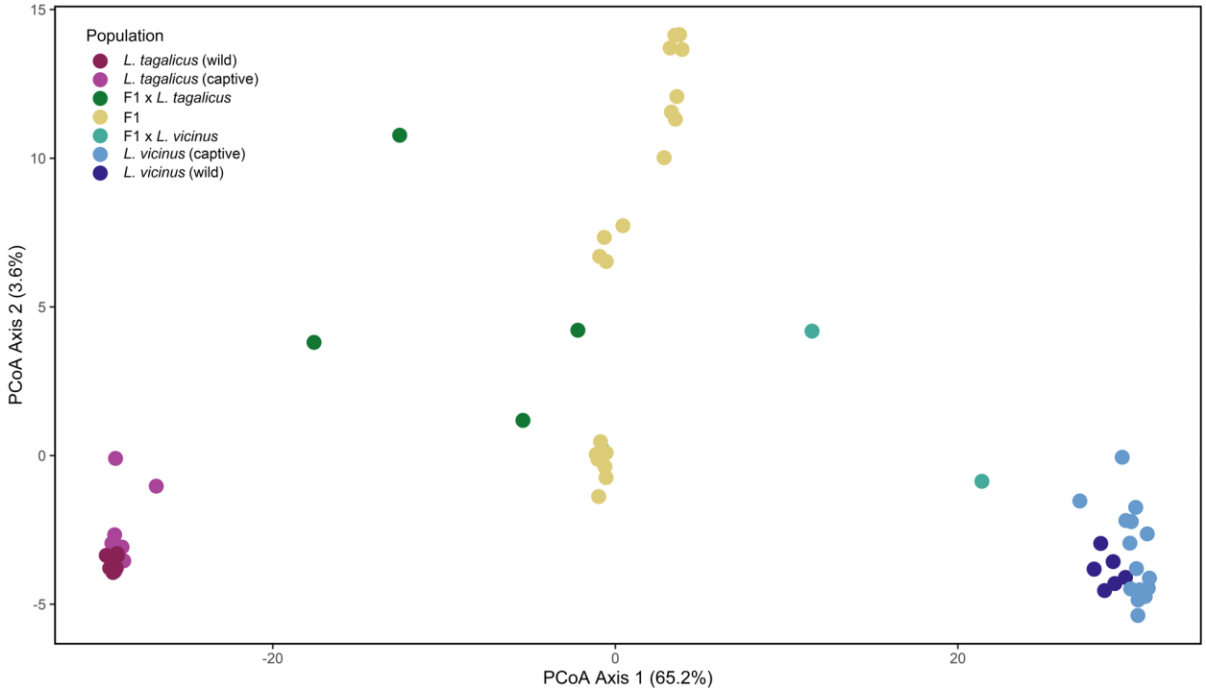


Figure 3. Principal Coordinates Analysis based on 6,077 SNPs for pure *L. tagalicus* (purple shades) and pure *L. vicinus* (blue shades) insects of wild-captured and captive-bred origin, and the offspring of different laboratory crosses (i.e. F_1 = mustard; backcrosses = green shades).

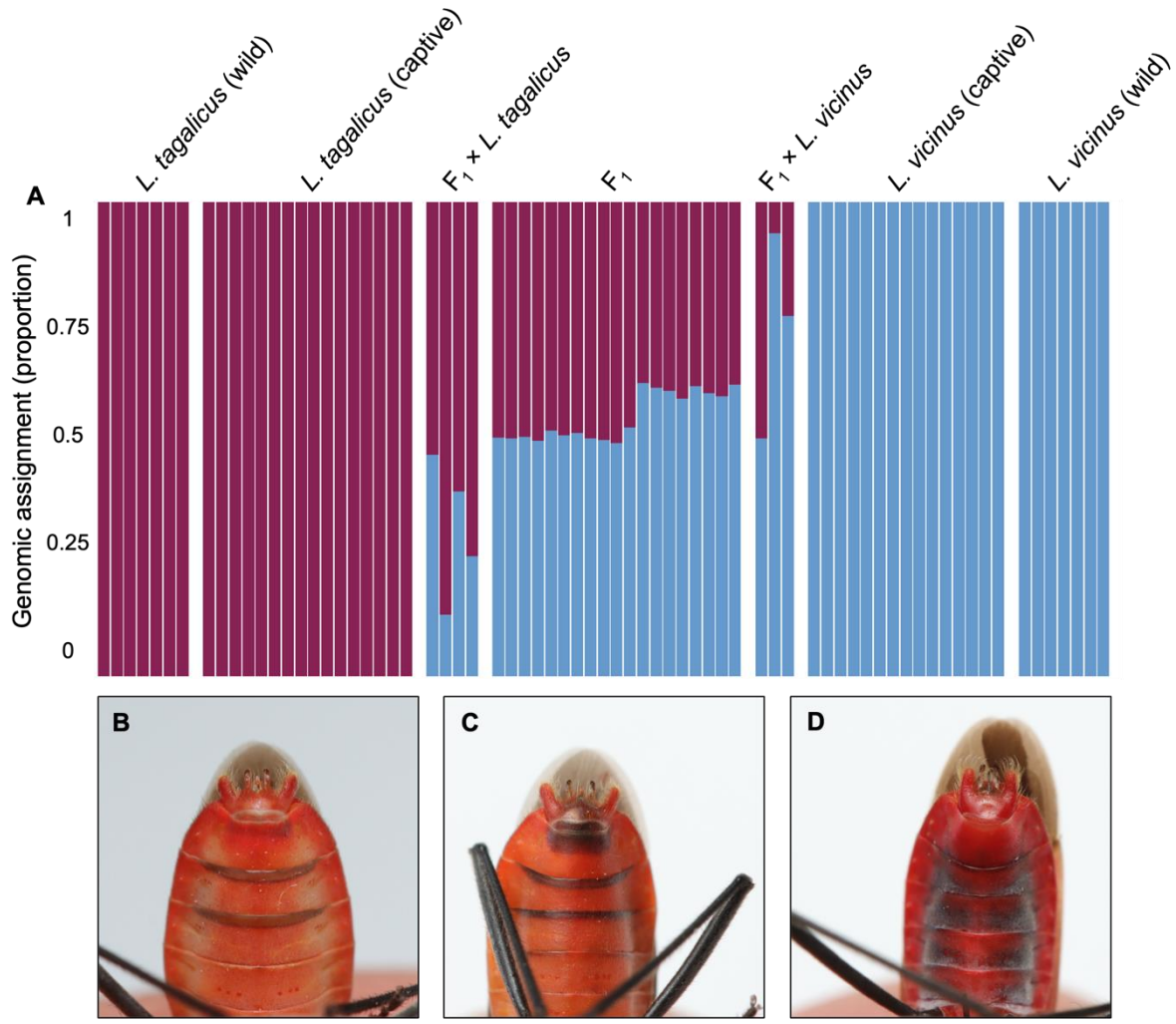


Figure 4. (A) Admixture plot showing the proportion of each individual insect's genomic assignment (y-axis) to the two inferred genetic clusters for different parental populations and crosses involving *Leptocoris tagalicus* and *L. vicinus*. The clusters indicated by purple and blue correspond to *L. tagalicus* and *L. vicinus,* respectively. Photographs of male genitalia are included for pure *L. tagalicus* (B), a F_1 hybrid between *L. vicinus* and *L. tagalicus* (C) and pure *L. vicinus* (D).

Discussion

Range shifts in Leptocoris soapberry bugs may follow human-mediated host plant dispersal

We found evidence in support of our hypothesis that human-mediated introductions and movements of Sapindaceae plants may underlie changes in the distributions of *Leptocoris* soapberry bugs in Australia and South Africa. In Australia, introduced *L. vicinus* is still restricted to the vicinity of Darwin on public plantings of its currently sole known host plant in the country, alien *Schleichera oleosa*, more than 60 years after its initial discovery (Carroll et al., 2005b). However, other host plant species present in the NT and the east coast of Australia include those known to be utilised by *L. vicinus*, such as *Koelreuteria elegans* and *C. halicacabum* (Carroll and Loye (2012), Li et al. (2025)). This suggests that the insect may spread beyond its current population in Darwin.

We recorded *L. rufomarginatus* far outside (500km south) of its previously published distribution (Carroll et al., 2005b). At two sites we observed it feeding on *A. coriaceous,* a new host record for the insect. Only one of our observations occurred within the previously reported natural range of *A. tomentosus*. Together with ALA occurrence records of the known host plant species for *L. rufomarginatus*, our findings suggest that the insect may have undergone a range shift facilitated by the introduction and subsequent spread of native host plants beyond their prior ranges, particularly associated with extralimital plantings in the Sydney region, where the density of host records was relatively high. However, we note that it remains unclear whether the previously reported southernmost observations of *L. rufomarginatus* represented a limit of the species–rather than the limit of sampling–or if the species has recently expanded further within the natural range of its hosts, e.g., as a result of climate change.

In South Africa, the presence of *L. mutilatus* in the Western Cape is intriguing, as its historical native range lies in the northeastern regions of the country. Our records from around Cape Town are therefore more than 1000km outside the species' previously known range (Göllner-Scheiding, 2008). We also provide the first record of *L. mutilatus* feeding on an *Alectryon* species. In the Western Cape province, almost all the *L. mutilatus* insects were short-winged (i.e., flightless), while those collected

from native *C. corindum* and invasive *C. halicacabum* in Kruger National Park were mostly volant (i.e., long-winged). In North America, the soapberry bug *Jadera haematoloma* evolved greater fecundity on invasive *Koelreuteria elegans*, likely as a response to annually cycling seed crops produced by this host plant (Carroll et al., 2003). These rapid evolutionary responses have been partly attributed to an increase in flightless and rapidly cycling morphs in *J. haematoloma* (Carroll et al., 2003). For *L. mutilatus* in South Africa, it is therefore possible that pre-existing flight life history polyphenism facilitated the discovery of new host patches (i.e., by highly volant individuals) followed by a subsequent increase in flightless morphs that are best suited for exploiting the cyclical seed production by the new host plants. We note that the insects collected from *A. connatus* had proboscides that were significantly shorter than those of insects from the native range and that proboscis length was larger than the distance-to-seed-centre in these insects. This may hint towards evolutionary responses in the insect on this host plant and deserves future research. How these insects made it to the Western Cape province remains unknown. *Leptocoris hexophthalmus* occurs naturally in the Western Cape province (Picker et al., 2019) and future work should investigate whether it can hybridise with *L. mutilatus* under field or laboratory conditions. Putative hybrids involving *L. mutilatus* (and possibly *L. amictus*) have been identified on invasive *C. grandiflorum* along South Africa's east coast, in the KwaZulu Natal province (SPC, personal observation), suggesting that hybridisation between different *Leptocoris* species is likely to occur in South Africa where they co-occur.

The potential evolutionary impacts on Leptocoris species in Australia

Our hybridisation experiment demonstrated that alien *L. vicinus* in Australia can hybridise with native *L. tagalicus,* with F_1 hybrids able to produce viable offspring only when backcrossed with either parental species. Thus, if these two species do come into contact in the wild and hybridise, introgression is likely to occur. This could lead to "genetic pollution" of the native insect's gene pool (e.g., see Stephens et al. (2020)). There are circumstances that may facilitate this. First, temporal variation in the availability of the fruits of different host plants (especially for *L. vicinus* living on a single tree) could make insects reliant on searching for suitable host plants further afield. This may facilitate contact between different species, hybridisation, and backcrossing with *L. tagalicus* (Dufresnes et al., 2020). The founding size of the *L. vicinus* population

in Darwin is unknown, but we detected high levels of inbreeding in the current population (n = 7 individuals; F_{IS} = 0.32, results not shown). Given its geographic isolation and likely low genetic diversity, this population may benefit from introgressive hybridisation. It should be noted that our experiments did not test for viability of backcrossed offspring. As a shared host of *L. tagalicus* and *L. vicinus* (Carroll and Loye, 2012, Carroll et al., 2005b), invasive *C. halicacabum* is the most likely host plant to enable contact between the two insect species. *Cardiospermum halicacabum* is invading the tropical savannahs of Qld and the NT, including nearby the *L. vicinus* population in Darwin (Le Roux et al., 2025b). Future surveys across the greater Darwin region should also seek to identify additional plantings of the alien *Schleichera oleosa*.

Our attempts to hybridise *L. tagalicus* or *L. vicinus* with *L. rufomarginatus* were unsuccessful. In all pairings, females produced eggs but none of these hatched and no copulation attempts were observed over the course of our experiments. The soapberry bug *J. haematoloma* is known to produce infertile eggs in the absence of copulation (Carroll, 1991), and we observed virgin females of all three captive *Leptocoris* species, kept in isolation since the 4-5th instar stage, to lay eggs that never hatched. Therefore, the presence of eggs does not necessary indicate post-zygotic isolation. *Leptocoris rufomarginatus* is highly arboreal and much larger and longer-legged compared to the two other species and may be genetically as well as morphologically (i.e., genitalia) too divergent from the smaller bodied *L. tagalicus* and *L. vicinus* to successfully hybridise (Gross 1960). While it is therefore unlikely that the range expansion of *L. rufomarginatus* will have any genetic implications on congeners via introgressive hybridisation, the lower availability of host plants at these range margins may result in increased competition with other soapberry bug species, particularly the more abundant *L. tagalicus*. Such competition may slow or limit the expansion (Legault et al., 2020) of *L. rufomarginatus,* which has not yet been found to utilise the more abundant invasive hosts that *L. tagalicus* has adapted to exploit (e.g., *C. grandiflorum*), compared to its native host plants in the region.

Conclusion

The results of our field collections and breeding experiments show that anthropogenic changes in host plant distributions are impacting *Leptocoris* species, with the potential for significant evolutionary effects via local adaptation and

interspecies hybridisation by the insects. While the current study highlights the distributional changes of soapberry bugs in both Australia and South Africa due to the human mediated expansion and introduction of their host plants, it is likely that soapberry bugs are experiencing similar changes elsewhere in the world. The soapberry bug play in Australia and South Africa has taken the stage worldwide, often involving the same actors, i.e., repeated invasions by the same host plant species and subsequent colonisation by different native soapberry bugs on different continents. For example, invasive *Cardiospermum* species native to the Americas and *Koelreuteria* species native to Asia, have now been recorded from every continent except Antarctica (GBIF Secretariat 2023a, GBIF Secretariat 2023b) and, in many instances, they have been colonised by native soapberry bugs (Carroll and Loye 2012)

Our study highlights the diverse ways in which human activities influence the distribution, ecology, and evolutionary dynamics of soapberry bugs. The continued spread of alien and extralimital native host plants is likely to shape the global distribution of these insects. Future research should explore whether hybridisation occurs among other soapberry bug species, and whether this process is promoted by alien, naturalised or invasive Sapindaceae species. Finally, the numerous cases of novel interactions between soapberry bugs and alien host plants, together with their rapid evolutionary responses, provide a unique opportunity to examine the ecological and genomic mechanisms driving rapid evolution in the Anthropocene.

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Data accessibility statement

Raw insect trait and genotype data will be made available upon acceptance of the paper in the Zenodo online repository.

Competing interests statement

The authors have no competing interests to declare.

Author contributions

Levi Brown – Conceptualisation, Methodology, Validation, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing. **Dylan M. Geraghty** – Conceptualisation, Methodology, Validation, Investigation, Data Curation, Writing – Review and Editing. **Maria Lambos** – Investigation, Data Curation, Writing – Review and Editing. **Jessica O'Hare** – Formal Analysis, Data Curation, Writing – Review and Editing. **Scott P. Carroll** – Conceptualisation, Validation, Writing – Review and Editing, Funding Acquisition. **Johannes J. Le Roux** – Conceptualisation, Methodology, Validation, Formal analysis, Data Curation, Writing – Original Draft, Writing – Review and Editing, Funding Acquisition.

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