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ORIGINAL PAPER

Genetic insights into the invasion success of a non-native weed: the case of stinking passionflower (*Passiflora foetida* sens. lat.) in Australia

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Abstract The persistence and range expansion of non-native invasive species is in part due to their genetic potential for adaptation in new environments, often associated with reduced competition or predation. The success of a non-native population can be dependent on the initial number of colonising individuals and their genetic diversity, either through the initial introduction or subsequently via multiple introductions across time and space. This study presents research on *Passiflora foetida* sensu lato, demonstrating the value of analysing the nuclear genome of a non-native invasive weed to complement findings from chloroplast genome analysis. *Passiflora foetida* is native to the Neotropics, and is a threatening invasive weed targeted for management across northern Australia. Biological control is being explored as a long-term strategy with success more likely when agent selection is informed by introduction history, genetic lineage distribution, and origin of populations of the target weed. This detailed study into the nuclear genomics of *P. foetida* sensu lato across its non-native range in Australia aimed to determine (1) if the nuclear genome supports earlier genetic insight from chloroplast genome analysis suggesting that there are three genetic entities present in Australia, (2) the distribution of these identified entities, (3) if these entities are segregated or co-located at sites and (4) if there is any evidence of hybridisation. Our nuclear genetic analysis concurred with the chloroplast genome analysis on the presence of three separate genetic entities of *P. foetida* s. l. in Australia. Several locations were found to have multiple genetic entities present, but limited hybridisation was found between genetic entities. The extensive invasion of *P. foetida* s.l. in Australia is predominantly being driven by a single entity with very low levels of diversity, as the other two entities had localised distributions in eastern Australia. The low genetic variation present in *P. foetida* s.l. across the non-native range, and in the

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regions where the greatest threats from this weed are observed, enables for biological control solutions to be targeted to this entity.

Keywords Adaptive · Fitness · Genetic diversity · Hybridisation · Introductions · Invasion

Introduction

Ecological, evolutionary, environmental, and anthropogenic processes, both past and present, shape genetic diversity and population structure of species by influencing gene flow and demographic patterns (Loveless and Hamrick 1984; Hamrick and Godt 1996). The establishment success of a non-native species is influenced by the initial number of colonising individuals, the genetic diversity of the initial introduction, or the occurrence of multiple introductions across time and space (Dlugosh and Parker 2008; Szűcs et al. 2017; Kaňuch et al. 2021). The persistence and range expansion of non-native invasive species is in part due to the genetic potential for adaptation in new environments (Lawson Handley et al. 2011) and is often facilitated by reduced competition or predation (Mack et al. 2000; Wolfe 2002).

Genetic diversity plays a critical role in the establishment and persistence of invasive species, enhancing their capacity to adapt to novel environments through selection and plasticity (Booy et al. 2000). While high diversity and large founding populations are often associated with invasion success (Szűcs et al. 2017; Kaňuch et al. 2021), significant invasions can also occur despite the genetic bottlenecks and low diversity that typically result from small founder populations (Dlugosh and Parker 2008). Selection for preadapted genotypes may further reduce diversity if only the fittest persist (Mack et al. 2000). Conversely, high diversity in non-native ranges can result from introductions involving large founder size and/or genetically diverse individuals, or admixture among differentiated source populations (Novak and Mack 1993; Genton et al. 2005; Dlugosh and Parker 2008; Pairon et al. 2010; Smith et al. 2020). Even a few founders can maintain high diversity if they originate from genetically or geographically distinct populations. Hybridisation between previously isolated lineages or taxa can also generate novel diversity and enhance fitness, as seen in *Carpobrotus* hybrids outperforming native congeners (Vilà and D'Antonio 1998; Hovick and Whitney 2014; Buhk and Thielsch 2015). Although initial hybrids may not have high fitness, ongoing recombination through generations (e.g. F_2 and backcrosses) can produce genotypes with increased invasiveness (Li et al. 2021). Admixture may also overcome mate limitation in small founder populations, facilitating establishment and invasion (Mesgaran et al. 2016), and under strong post-introduction selection, such genetic mixing can drive rapid evolutionary change (Bossdorf et al. 2005; Oduor et al. 2011; Turner et al. 2014).

Knowledge of origins of populations, and identification of genetic lineages and their distribution across a non-native range, can assist with targeting of the biocontrol agent search and selection of better adapted candidate biocontrol agents that are more likely to be effective (Gaskin et al. 2011; Moody et al. 2016; Kwong et al. 2017; Morin 2020). Here we present research on *Passiflora foetida* sensu lato (hereafter *P. foetida*) that demonstrates the benefit of analysing the nuclear genome of a non-native invasive weed to complement results from a chloroplast genome analysis. The chloroplast genome is maternally inherited with diversity that is often geographically based and more conserved than the nuclear genome, so is useful for determining the identity of introductions (Wolfe et al. 1987). Analysis of the nuclear genome will show more contemporary relationships among individuals and populations, including identifying any hybridisation that may be occurring (Wolfe et al. 1987).

Passiflora foetida is a fast-growing vine native to Central and South America that climbs over vegetation, including trees, and smothers plant communities (Lohr et al. 2016; Jucker et al. 2020). It has been widely introduced across many regions of the world, including South-East Asia, South Pacific Islands, China, Hawaii, India, Madagascar and Australia (Yockteng et al. 2011). In Australia it is commonly referred to as stinking passionflower, and is a threatening invasive weed targeted for management across northern Australia (Jucker et al. 2020). Its non-native distribution in Australia spans a broad range of ecosystems across northern regions, including monsoonal, wet tropical and sub-tropical climates, as well as riparian and coastal regions in hotter, drier deserts and grasslands. It is in the drier more monsoonal regions where *P. foetida* represents a greater

threat to environmental values. Traits that facilitate invasiveness include (1) almost no limitation on seed dispersal, (2) fruit production within 3 months of germination and year-round fruiting with sufficient soil moisture, (3) the ability to build up dense vegetation smothering mats within a single season, (4) the ability to over-top large trees, (5) a notable absence of damaging native pests and pathogens, (6) the ability to not only enhance fire intensity but survive fires via canopy-stored seed and below-ground crowns, and (7) rapid post-fire regeneration that further suppresses native vegetation (Webber et al. 2014). Moreover, experienced weed ecologists have expressed concern about a noticeable change in the prevalence and spread of this weed across the western part of its Australian distribution in the past two decades (Lohr et al. 2016).Physical and chemical control of *P. foetida* has minimal impact on long-term management outcomes as it is either unfeasible due to the scale and growth rates of infested areas, or not justifiable due to off-target impacts on associated flora and fauna (Jucker et al. 2020). Biological control is being considered as a means of providing a long-term solution to mitigate the negative impacts of this weed in Australia (Webber et al. 2016; Betancur-García et al. 2024). Success of biocontrol programs can be variable due to the complexity of multiple factors involved and are best implemented based on information on the introduction history of the invasive species (Harms et al. 2020). Understanding the spatial distribution of distinct genetic entities can also inform management design for improved control, such as where buffer zones are positioned to avoid different variants moving to new areas (Moore et al. 2008).

Our previous study using whole chloroplast sequencing of *P. foetida* has shown that there are three genetic entities present in Australia, and that these correspond to likely introductions from Ecuador, Brazil and the Caribbean (Hopley et al. 2021). This initial work was focussed on identification of areas of origin and was limited to single individuals from each of 36 locations, thus it was not able to reveal whether this diversity was also reflected in the nuclear genome, or whether there was more fine scale variation within populations. To improve knowledge of the management of non-native *P. foetida* globally, we continued to investigate the Australian case study and undertook a detailed analysis of the nuclear genomics of the species. We aimed to determine (1) if the nuclear genome supports earlier genetic insight from chloroplast genome analysis suggesting that there are three genetic entities present in Australia, (2) the distribution of these identified entities, (3) if these entities are segregated or co-located at sites, and (4) if there is any evidence of hybridisation. This work highlights the benefits of combining both chloroplast and nuclear genome analyses to obtain comprehensive knowledge of the introduction and colonisation history of an invasive species.

Materials and methods

Study species

Passiflora foetida belongs to section Dysosmia, with approximately 30 taxa currently recognised (Vanderplank 2013; Svoboda and Ballard 2018). The section is taxonomically confusing, with no molecular phylogeny and two major species complexes (Vanderplank 2013; Svoboda 2018a, b; Svoboda and Ballard 2018). The latest revision of Dysosmia has both clarified and added to the uncertainty (Vanderplank 2013). Hybridisation between taxa within Dysosmia is known for co-occurring species in both native and non-native ranges (Vanderplank 2013). The native range for section Dysosmia broadly covers the Neotropics from the southern United States of America, through Central America and the Caribbean to Argentina and Uruguay, with centres of diversity in Brazil and Mexico (Vanderplank 2013). Collections from across the Australian range have been determined variously as *Passiflora foetida* L., *Passiflora foetida* L. var. *hispida* (DC ex Triana & Planchon) Killip ex Gleason (syn. *Passiflora vesicaria* L. var. *vesicaria*), *Passiflora foetida* L. var. *ellisonii* Vanderpl., and *Passiflora foetida* L. var *foetida* (Vanderplank 2013; Svoboda et al. 2016) (Atlas of Living Australia website at http://www.ala.org.au. Accessed 2021). A synthesis of this material suggests that the validity of many of these determinations may be questionable based on existing taxonomic circumscriptions (B.L. Webber, unpublished data; Ohlsen 2020).

In this study, we used the following morphometric characters to ascribe material to *P. foetida*: pubescent shallow tri-lobed leaves, glandular hairs on all vegetative parts, and ornate pinnatisect floral bracts with glandular tips. Often flowers and fruits were available

to confirm other useful diagnostic characters: white and mauve flowers, bracts highly pinnatisect covered with glandular tipped hairs, fruit green when unripe, becoming yellow (or occasionally remaining green) when ripe, seeds symmetrical and tridentate at the apex. It is recognised that many of these characters also fit other taxa within section Dysosmia (Vanderplank 2013), but are, in turn, unique to Dysosmia within the broader Passifloraceae (Svoboda 2018b). Resolution of the taxonomic uncertainty for *P. foetida* in Australia is beyond the scope of this study. For the purposes of this work, we refer to the entity(ies) present in Australia as *P. foetida* following the recommended national convention established by Ohlsen (2020).

Sampling

Leaf samples from at least five to twelve plants at a site were collected from 98 sites broadly distributed across the entire range of *P. foetida* in Australia, spanning a distance of c. 4500 km (east to west; Fig. 1). Samples were taken at least 10 m apart to prevent inadvertently sampling the same individual plant twice, given this is a possibility with this scrambling vine if samples were collected closer together. Leaf samples were placed in silica gel upon collection for preservation prior to DNA extraction.

Contig assembly

A reference genome for *P. foetida* was developed for alignment and identification of SNPs. A whole genome run was undertaken on a single individual of *P. foetida* sourced from near the Fitzroy River in the Danggu Geikie Gorge National Park, Australia (−18.11 S, 125.70 E) and representative of the dominant genetic entity as determined from previous work (Hopley et al. 2021). DNA extraction using a modified CTAB method (Doyle and Doyle 1987), with the addition of sodium sulfite (Byrne et al. 2001) and 1% w/v polyvinylpyrrolidone to the extraction buffer. Sequencing was undertaken at the Australian Genome Research Facility (AGRF) using TruSeq Nano library preparation and sequenced on the NovaSeq 6000. Fastp (Chen et al. 2018) was used to remove adapters, poor quality sequences (mean phred ≥ Q30), reads with < 20% complexity, reads shorter than 125 bases, and poly X and G trimming was enabled. A per read cut by quality was also undertaken with a sliding window size of 4 moved from front to tail with a mean quality of 20. Burrows-Wheeler Aligner

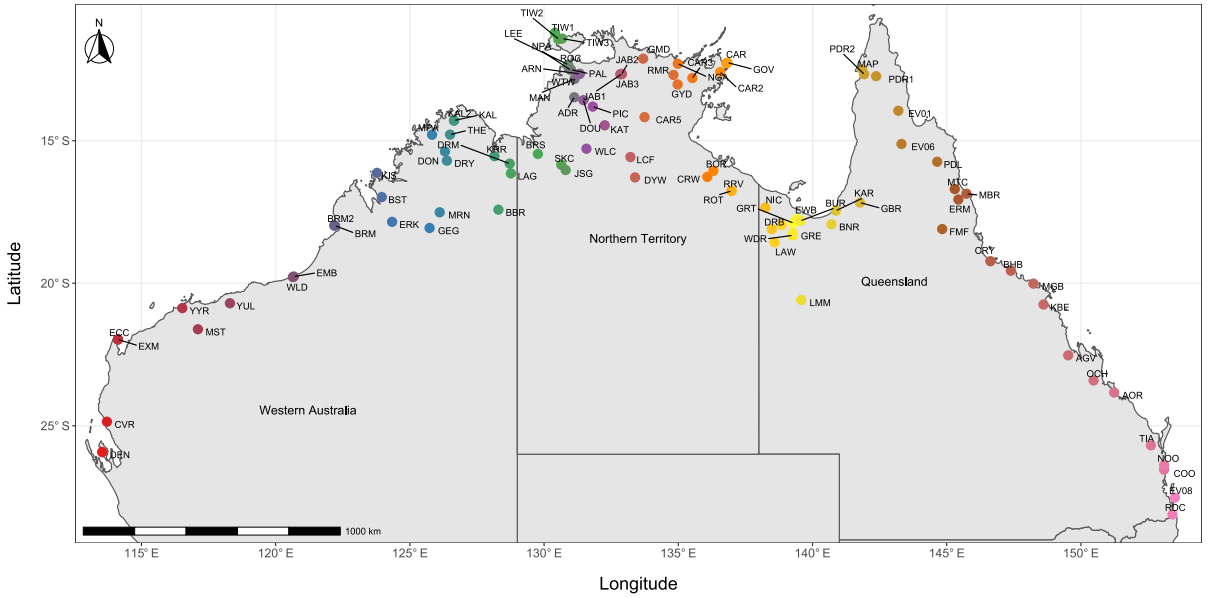


Fig. 1 Location of sampling sites in Australia, see Supplementary Information for details of site locations. Colours are used exclusively to distinguish sampling sites and correspond to those presented in Fig. 2; they do not represent any biological or analytical significance

(BWA; (Li and Durbin 2009)) was used to map cleaned and trimmed sequences to the *P. foetida* chloroplast genome (NC_043825.1); sequences that did not align to the chloroplast were assumed to be nuclear sequences and kept for further work. The retained sequences were assembled using MEGAHIT (v1.28; (Li et al. 2015)) and the resulting assembly contained 1,878,774 contigs (750 Mb) with lengths ranging between 200 bp and 153,334 bp.

SNP genotyping

Genomic DNA was extracted from 978 samples using a modified CTAB method (Doyle and Doyle 1987, with the addition of sodium sulfite (Byrne et al. 2001) and 1% w/v polyvinylpyrrolidone to the extraction buffer. DNA samples were then sent to Diversity Arrays Technology (Canberra) for DArTSeq analysis. DArTSeq analysis includes technical replicates to assess sequencing error, these are samples that after library preparation are sequenced twice, there were 198 technical replicates in the dataset. Sequences were filtered for quality and to remove adapters using the process_radtags program within STACKS (Catchen et al. 2011, 2013). The resulting sequences were aligned to the previously described contigs of *P. foetida* using BWA (Li and Durbin 2009), then filtered to remove low quality alignments and secondary reads using SAMTOOLS (Li and Durbin 2009). The final sequences were run through the ref_map pipeline for SNP calling, followed by the populations program to filter out SNPs with more than 90% missing data in STACKS. A custom script (Supplementary Information script) modified from Wright et al. (2019) was used to filter SNPs for read depth greater than 5 at both the reference and alternate alleles, a coverage difference of 60% (which removes SNPs that have disproportionate amplification of the reference or alternate allele), heterozygosity > 70% and reproducibility of < 90%. Repeat samples (technical replicates used for reproducibility estimates) were then removed from the dataset that was then filtered for minimum minor allele frequency of 1% and maximum missing data of 25% using VCFTOOLS (Danecek et al. 2011). The data was then read into R (R Core Team 2019) using vcfR (Knaus and Grünwald 2017) and filtered using dartR (Gruber et al. 2018) to sites that had at least five samples collected. Populations that had more than five individuals were subsampled to five representatives at that site to avoid any bias in results, this removed 488 samples from further analysis (Supplementary Information Table 1). Resulting data were then filtered to remove loci with missing data, the final dataset consisted of 490 individuals, representing 98 sites, and contained 9365 SNPs. To examine the genetic patterns in subsets of the data, a number of individuals were removed as detailed below. Individual samples were removed from the prefiltered dataset, after which the filtering steps described above were applied to each resulting subset.

Population structure, hybrid identification and genetic diversity

To identify clusters of individuals and visualise the major axes of variation between clusters, principal component analysis (PCA) was undertaken, implemented in the ADEGENET package (Jombart and Ahmed 2011) in R (R Core Team 2019). Jost's genetic distance was calculated using the MMOD (Winter 2012) package in R (R Core Team 2019).Population genetic structure was explored using STRUCTURE 2.3.4 (Pritchard et al. 2000), with ten independent runs for each K-value with a burn-in of 50,000 and 200,000 MCMC iterations. The R package POPHELPER (Francis 2017) was used to visualise results and select the most probable K based on the ΔK metric (Evanno et al. 2005).

Due to the presence of multiple genetic entities in the data, an analysis of potential hybrids was undertaken using NEWHYBRIDS (Anderson and Thompson 2002; Anderson 2003). Hybrid identification was run on a subset of 200 SNPs as this is the limit of the program. SNPs were selected using the gl.nhybrids function in R package DARTR (Gruber et al. 2018) that compares two sets of parental populations to identify loci exhibiting fixed allelic differences between the putative parental populations. NEWHYBRIDS was run with 10,000 sweeps for both burn-in and for computing actual Monte Carlo averages, and Jeffreys priors were applied.

Genetic diversity parameters were calculated in R (R Core Team 2019) with the DARTR (Gruber et al. 2018) package used for formatting data, expected and observed heterozygosity were assessed using ADEGENET (Jombart and Ahmed 2011), and POPPR (Kamvar et al. 2014) packages. Allelic richness was calculated using the POPGENREPORT package (Adamack

and Gruber 2014). GGPLOT2 (Wickham 2016) was also used for visualisation of results.

Results

Identification of genetic entities

The PCA results of all sampled sites (Fig. 2), confirmed the presence of three main genetic entities (as outlined in Hopley et al. 2021) and no new genetic entities. Note that genetic entity names refer to the majority of samples in the clade coming from the geographic area, however samples in the genetic entity are not exclusive to the named geographic area. The PCA groups represent: (1) the 'Brazil' genetic entity, which is differentiated along the first axis with positive values, which explains over 70% of the variation in the data; (2) the 'Caribbean' genetic entity, which is differentiated along the second axis with negative values and explains 11% of the variation; and (3) the 'Ecuador' genetic entity, represented by the majority of sampled sites, which was the geographically dominant genetic entity across the Australian range. Results of Jost's genetic distance analysis highlighted the differentiation between the three genetic entities (Fig. 3). The Brazil genetic entity (AGV, EV06 and MGB sites) had values of differentiation from the Ecuador genetic entity of 0.83, 0.83 and 0.69 respectively, with values amongst sites of the Ecuador genetic entity at or below 0.01. Jost's genetic distance values between sites in the Ecuador genetic entity and the Caribbean genetic entity, represented mainly by site LMM and to a lesser extent site MBR, were 0.28 and 0.12, respectively.

Distribution of genetic entities

Genetic cluster analysis on all samples using STRUCTURE found the strongest genetic split at two genetic

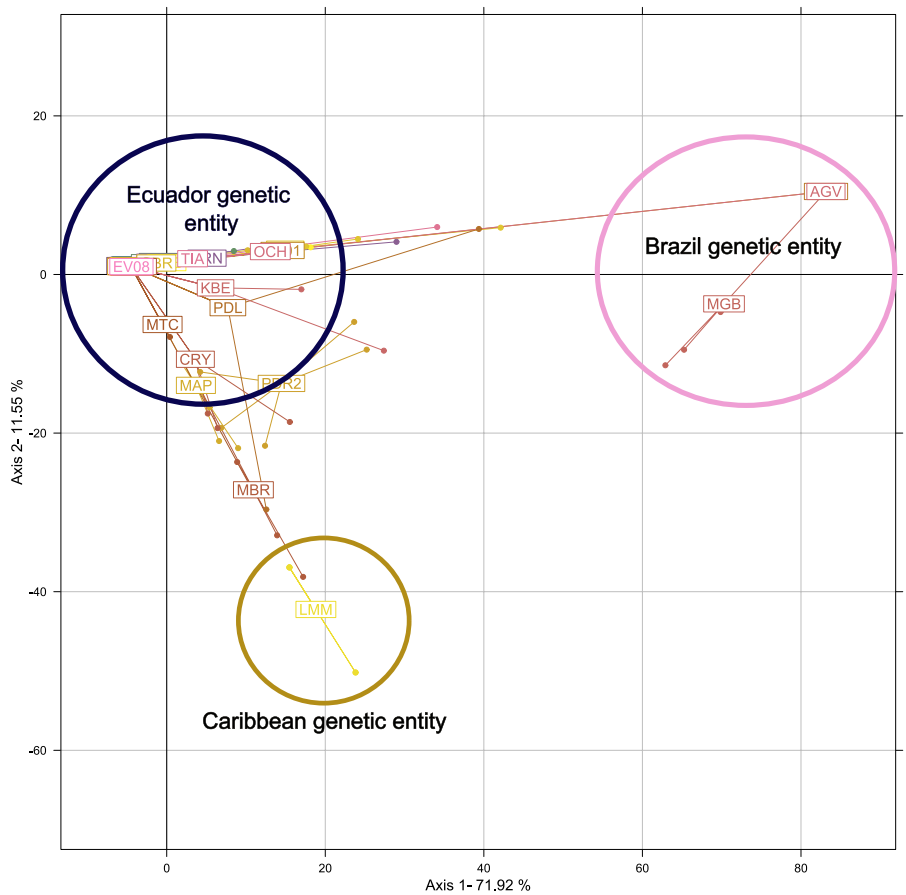


Fig. 2 Principal component analysis (PCA) plot based on genetic distance between individuals from all sites of *Passiflora foetida*. MBR, sitting outside the identified genetic entities represented by circles (genetic entities align to those identified in Hopley et al. 2021), is a mixed site that has individuals from both the Ecuador and Caribbean genetic entities. Colours used in plot correspond to those used in Fig. 1. Many sites in the plot overlap and therefore not all labels are displayed

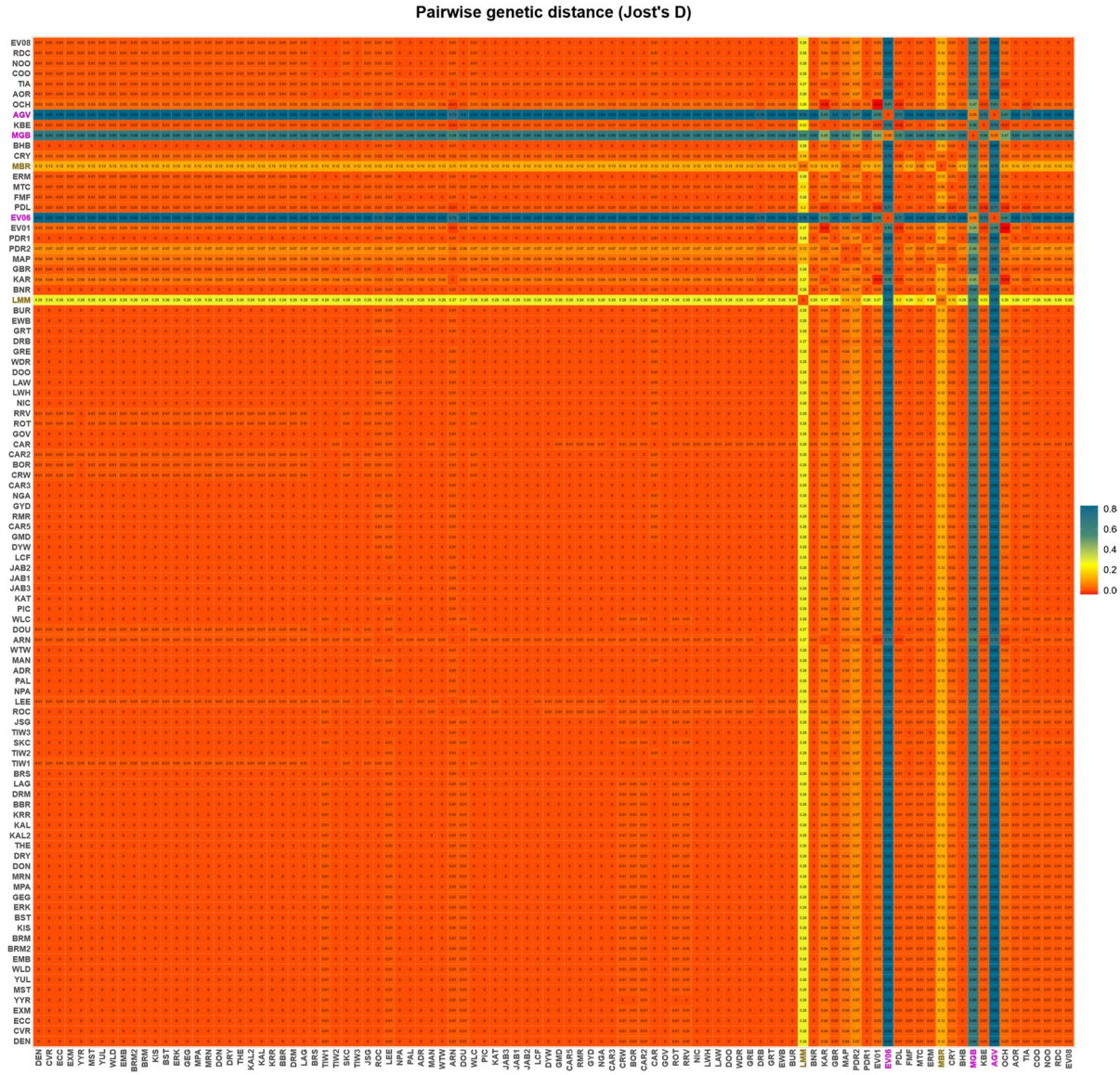
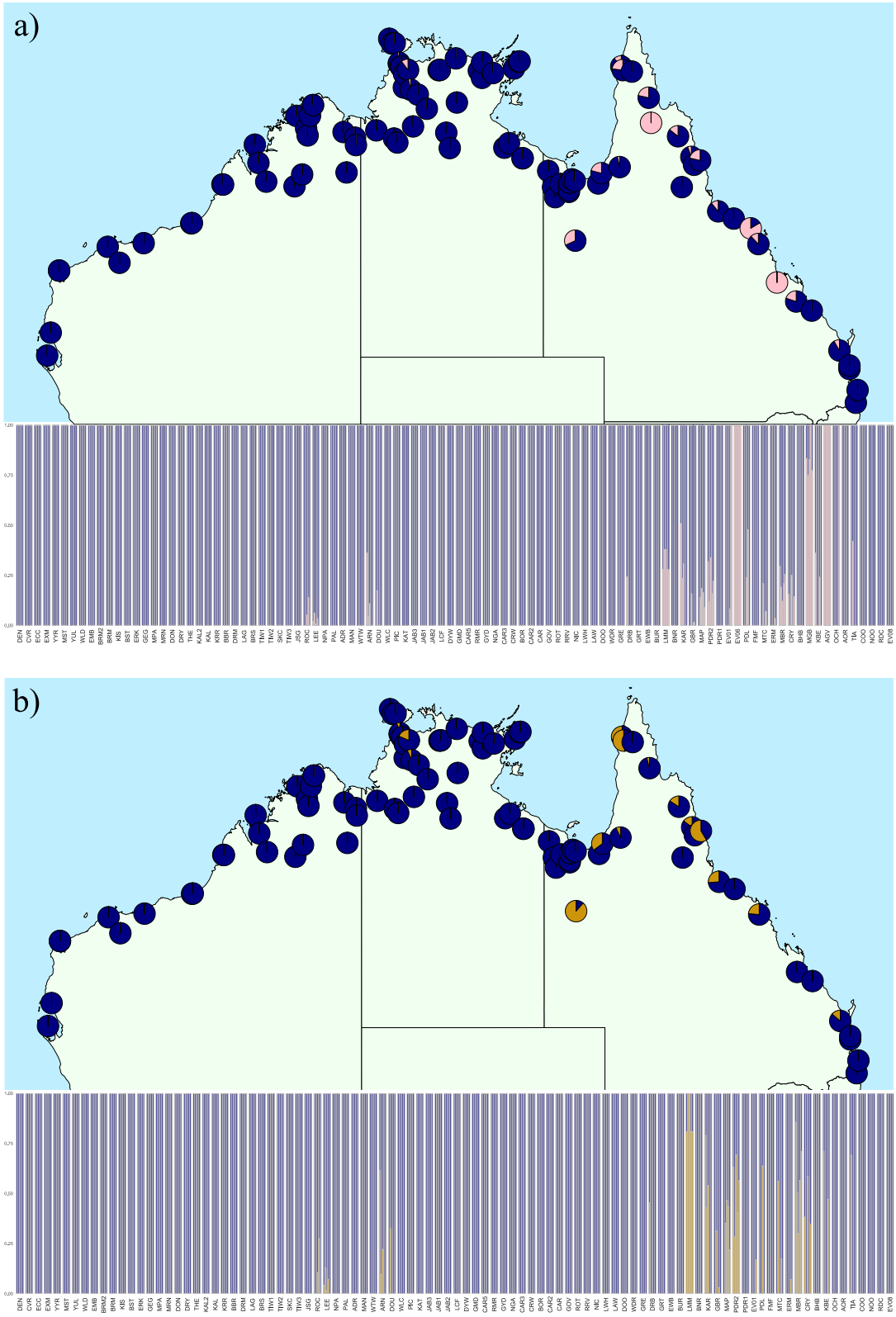


Fig. 3 Jost's genetic distance for all pairs of sampled sites of *Passiflora foetida*, sites are arranged West to East from left to right, orange indicates low differentiation, blue indicates high differentiation. Population labels are coloured to match the genetic entity they represent, Brazil genetic entity in pink, Caribbean genetic entity in khaki and the Ecuador genetic entity in black

clusters (Supplementary Information Fig. 1), the main cluster represented by the dominant Ecuador genetic entity (sites of pure navy blue) and the second genetic cluster represented by the Brazil genetic entity (sites of pure pink) (i.e. sites AGV, EV06 and MGB) (Fig. 4a). The STRUCTURE analysis also indicated admixture between the two genetic entities in several sites. As STRUCTURE identifies the dominant split in the data, in this case represented by the differentiation between the Ecuador and Brazil genetic entities, it can misrepresent another group as admixed individuals, and this is the case here as these admixed individuals represent the Caribbean genetic entity as elucidated from the PCA results. The Brazil genetic entity was found mainly in Queensland, with most sites with admixed individuals also occurring in Queensland.


a)
b)
1.00
0.75
0.50
0.25
0.00
DER CVR ECC EXM YYR MET YUL WLD EMB BRMM BRM KIB BST ERK GEG MPA MRN DON DRY THE KAL2 KAL KRR BBR DRM LAG BRS TIW1 TIW2 SKC TIM3 JAS ROC LEE NPA PAL AGN MAN WTW ARN DOU WIC PIC KAT JAB3 JAB1 JAB2 LCF DYW GMD CAR5 RMR GYD NGA CAR3 CRW BOR CAR2 CAR GOV ROT RRV WIL LWH LAW DOO WDR GRE DRB GRT EWB BUR LAM BNR KAR GBR MAP PSR2 PSR1 EV01 EV06 EDL FMF MTC ERM MBR CRY BHB MGB KBE AGV OCH AOR TIA COO NOO RDC EV08

◂**Fig. 4** Genetic clustering results from Structure analysis for **a** all sites and **b** sites aligned with Caribbean and Ecuador genetic entities for *Passiflora foetida*. Each individual sample within each site is represented by a vertical bar which is apportioned into its membership to each of the identified genetic clusters, each genetic cluster is represented by a different colour (Ecuador genetic entity = navy blue; Brazil genetic entity = pink; Caribbean genetic entity = gold)

The strong differentiation between the Brazil genetic entity and other genetic entities indicates this is likely a separate taxon. To further examine the genetic patterns this genetic entity was removed from the dataset and the data were reanalysed.

After removal of the individuals of the Brazil genetic entity, the remaining dataset consisted of 472 individuals representing 95 sites with 9631 SNPs. Removing the Brazil genetic entity more clearly highlighted the genetic difference between the Ecuador and Caribbean genetic entities. Genetic cluster analysis results again found the strongest genetic split at two genetic clusters (Supplementary Information Fig. 2), the main cluster represented by the dominant genetic Ecuador genetic entity (navy blue) and the second genetic cluster represented by the Caribbean genetic entity (gold), mainly site LMM (Fig. 4b). Several sites (PDR2, KAR, MBR, MAP, CRY) show high levels of admixture between the genetic entities. Again, the Caribbean genetic entity is mainly located within Queensland in the eastern spatial extent of the species complex in Australia. While the majority of admixed sites also occur in Queensland, there are a few sites, with a small portion of the second genetic cluster, which is associated with the Caribbean genetic entity, that occur in the Northwestern part Northern Territory close to Darwin (Fig. 4b).

Admixture among genetic entities

Initial hybrid analysis to investigate potential hybridisation between the Brazil genetic entity and the two other genetic entities allowed the identification of likely hybrids between genetic entities, where the Brazil genetic entity was represented by site AGV, and the other 'parent' was represented by the dominant Ecuador genetic entity site RDC. The results of this analysis (Fig. 5a) are consistent with the PCA, genetic distance and structure results, with sites AGV, EV06 and MGB assigned to the Brazil genetic entity, as were single individuals from site OCH and EV01. A single F1 hybrid between the genetic entities was identified in site PDL, and no F1 backcrosses with the Brazil genetic entity were identified. Fourteen individuals were assigned as F2 hybrids (Fig. 5a, all individuals (5) in LMM, one individual from each of: ARN, MBR, KBE, TIA, MTC and two individuals from each of KAR and PDR2), and, as with the Structure results, these individuals are either from the Caribbean genetic entity or admixed. These results confirm that there are sites in Australia with mixed genetic entities; however, with only a single individual assigned as an F1 hybrid, and no identified backcrosses, hybridisation between these genetic entities seems to only result in rare contributions to the adults at a site. Individuals assigned to the Brazil genetic entity, that were either an F1 hybrid between genetic entities or a backcross with the Brazil genetic entity (i.e. F1 × Brazil), were removed from the dataset for further analysis.

Hybrid analysis of the Caribbean genetic entity that was represented by site LMM, and the Ecuador genetic entity that was represented by site RDC, show all individuals in site LMM were assigned to the Caribbean genetic entity, as was a single individual from site MBR (Fig. 5b). A single F1 hybrid between the genetic entities was identified in site CRY, six F1 backcrosses with the Caribbean genetic entity were identified, three from MBR, and a single individual in sites PDL, PDR2 and MTC. Ten F2 hybrids were assigned; a single individual in sites KAR, KBE, MBR and TIA, two from CRY, and four individuals in sites MAP and PDR2. There were also nine F1 backcrosses with the Ecuador genetic entity, two from KAR, and one from each of ARN, DOU, DRB, GBR, KBE, MTC and ROC. These results indicate that there are sites with mixed genetic entities and higher numbers of hybrids and backcrosses between the Ecuador and Caribbean genetic entities than in those sites that involved the Brazil genetic entity. Most sites that have individuals with admixture involving the Caribbean genetic entity are located in Queensland, and three sites with a single individual that is a F1 backcross with the Ecuador genetic entity were present in the Northern Territory in the Darwin region. Individuals that were either (a) assigned to the Caribbean genetic entity, (b) an F1 hybrid between genetic entities, or (c) a backcross, were removed from the dataset for further analysis focusing on the dominant Ecuador genetic entity.

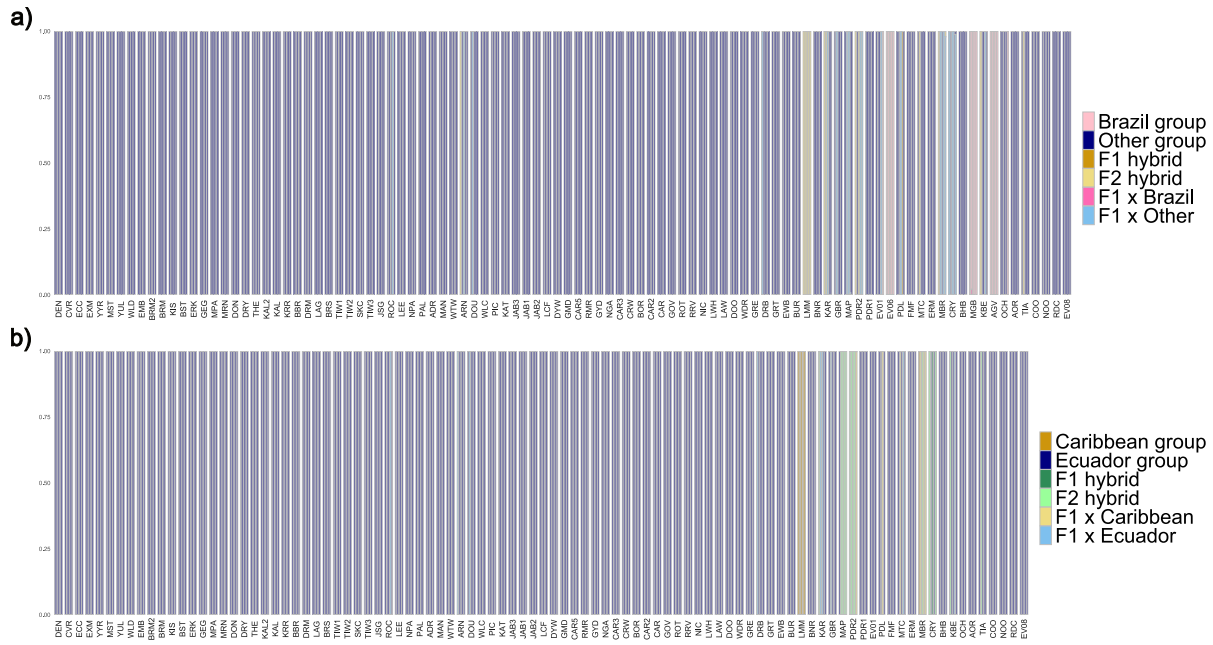


Fig. 5 Results of hybrid analysis for **a** all sites and **b** Caribbean and Ecuador genetic entities for *Passiflora foetida*. Each individual sample within each site is represented by a vertical bar coloured by its assignment to each of six membership classes: two parent genetic entities, F1s, F2s, and backcrosses to each parent genetic entity

Diversity across Australia

Our results revealed that a single genetic entity (i.e. the Ecuador genetic entity) is dominant across the Australian range, and as this corresponds with the areas in which local ecologists have been worried about a recent increase in invasiveness, we explored variation within this genetic entity and how that variation is structured. The dataset of the Ecuador genetic entity had 503 SNPs present in 431 individuals from 89 sites.

While only a small number of SNPs remained in the dataset, strong structuring was found across the samples based on PCA analysis that split sites into several groups (Fig. 6). A group of 29 sites were clustered along the first axis, explaining 44% of the variation, with negative values (below − 4, overlapping in the plot was difficult to perceive) and these sites represent all Western Australian sites and four sites across the border into Northern Territory, BRS, SKC, JSG and WLC (see Fig. 1). A group of 11 sites were clustered along the second axis, explaining 23% of the variation, also with negative values (below − 4, again overlapping in the plot so difficult to detect), and all these sites are at the eastern extent of the distribution (sites in the southeastern corner of Queensland: OCH, AOR, TIA, COO, NOO, RDC, EV08 and some sites in the northeast of Queensland: EV01, PDL, FMF, ERM; see Fig. 1). The rest of the sites were spread between these groups in ordination space, and individuals within these sites exhibited more variation than those in the previously identified groups (Fig. 6).

Measures of Jost's genetic distance ranged from 0 to 0.19 and showed a greater spread of values than in previous datasets (Fig. 7). There are three groups of sites with no or very low genetic differentiation, and these represent the group of sites in the west and two groups of sites in the east that were identified in the PCA results. Structure results support two clusters (Supplementary Information Fig. 3) with a strong demarcation between the sites west of Darwin and those east of Darwin, with these sites showing varying levels of admixture between the two identified genetic clusters (Fig. 8). Observed heterozygosity ranged from 0 to 0.243 (Fig. 9, Supplementary Information Table 1), and was generally low across most sites, with 80 sites having values

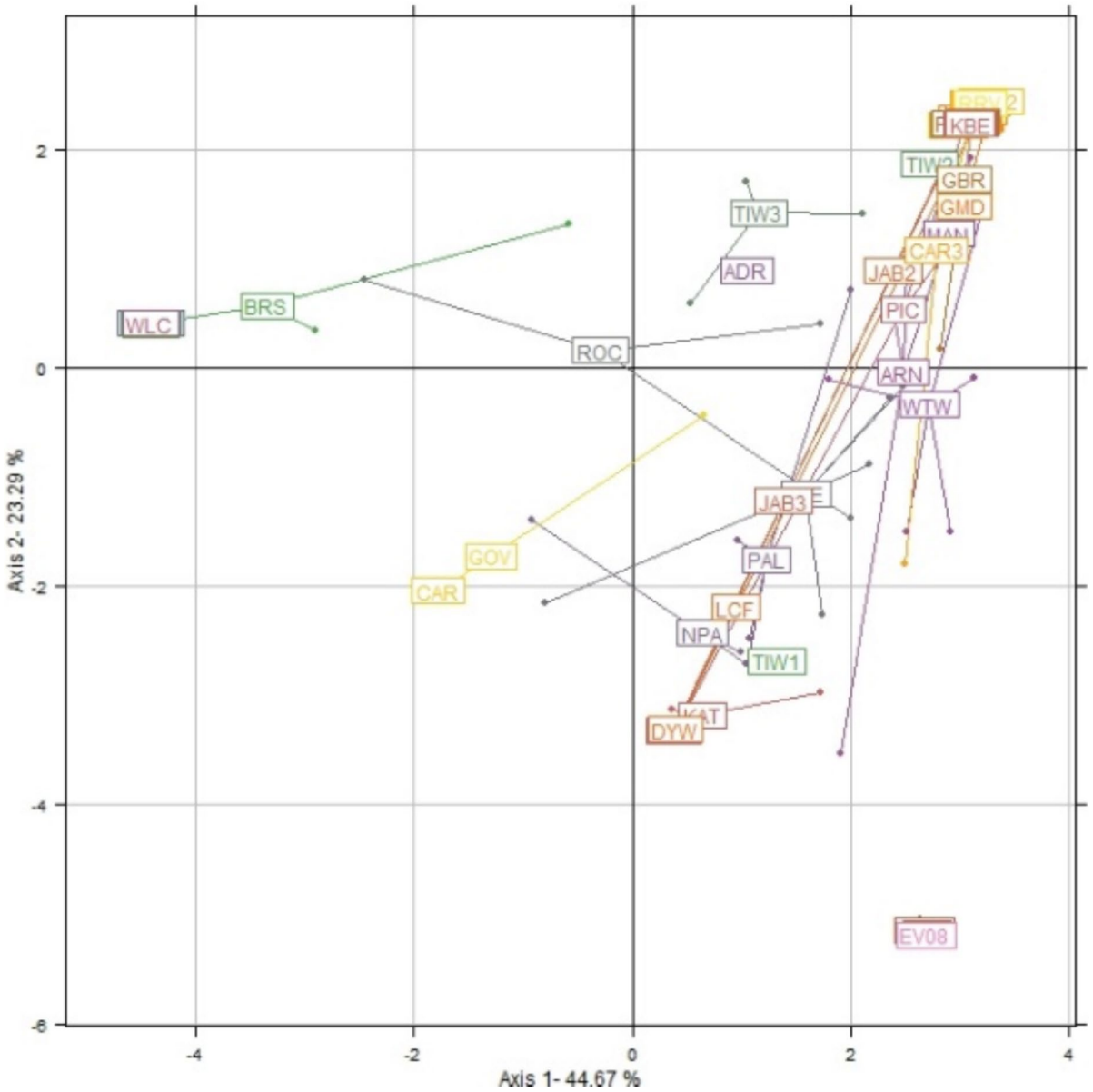


Fig. 6 Principal component analysis (PCA) plot for Ecuador genetic entity sites of *Passiflora foetida*

below 0.01. Two sites in the Northern Territory near Darwin, ARN and LEE, that show admixture in the structure plot have higher values of 0.15 and 0.24 respectively. Interestingly, other sites with admixture show low diversity with values below 0.0. Similar patterns were seen in expected heterozygosity, which ranged from 0 to 0.331 (Supplementary Information Table 1) and was generally low across most sites, with 70 sites having values below 0.01. Allelic richness ranged from 1 to 1.686 (Supplementary Information Table 1), and was low across most sites, with 80 sites having values below 1.1. Expected heterozygosity was higher than observed heterozygosity in 17 of the 89 populations, all in the Northern Territory sites. All sites in Western Australia show low diversity with expected heterozygosity values from 0 to 0.003 and observed heterozygosity values from 0 to 0.004.



Fig. 7 Jost's genetic distance for pairs of Ecuador genetic entity sites of Passiflora foetida. Sites are arranged West to East from left to right, orange indicates low differentiation, blue indicates high differentiation

Discussion

Three separate genetic entities of *P. foetida* were recognised with nuclear genome analysis and these matched the three genetic entities identified from earlier analysis of the chloroplast genome using herbarium samples from the native range (Hopley et al. 2021). In the present study, the presence of all three genetic entities was confirmed, however the spatial distribution of each was quite different. The Ecuador genetic entity was the most common genetic entity identified and was present in most sites sampled across the non-native Australian range. In contrast, the Brazil and Caribbean genetic entities were present at fewer locations, mainly within Queensland in the eastern distribution of the species in Australia. These results suggest that the Ecuador genetic entity may have become dominant through introduction history and initial abundance that contributed to dominance through founder effects and early establishment (Buckley et al. 2007; Szűcs et al. 2017; Gioria et al. 2023), and through disturbance regimes that favoured rapid recovery or colonisation. It is also possible that the Ecuador genetic entity has traits

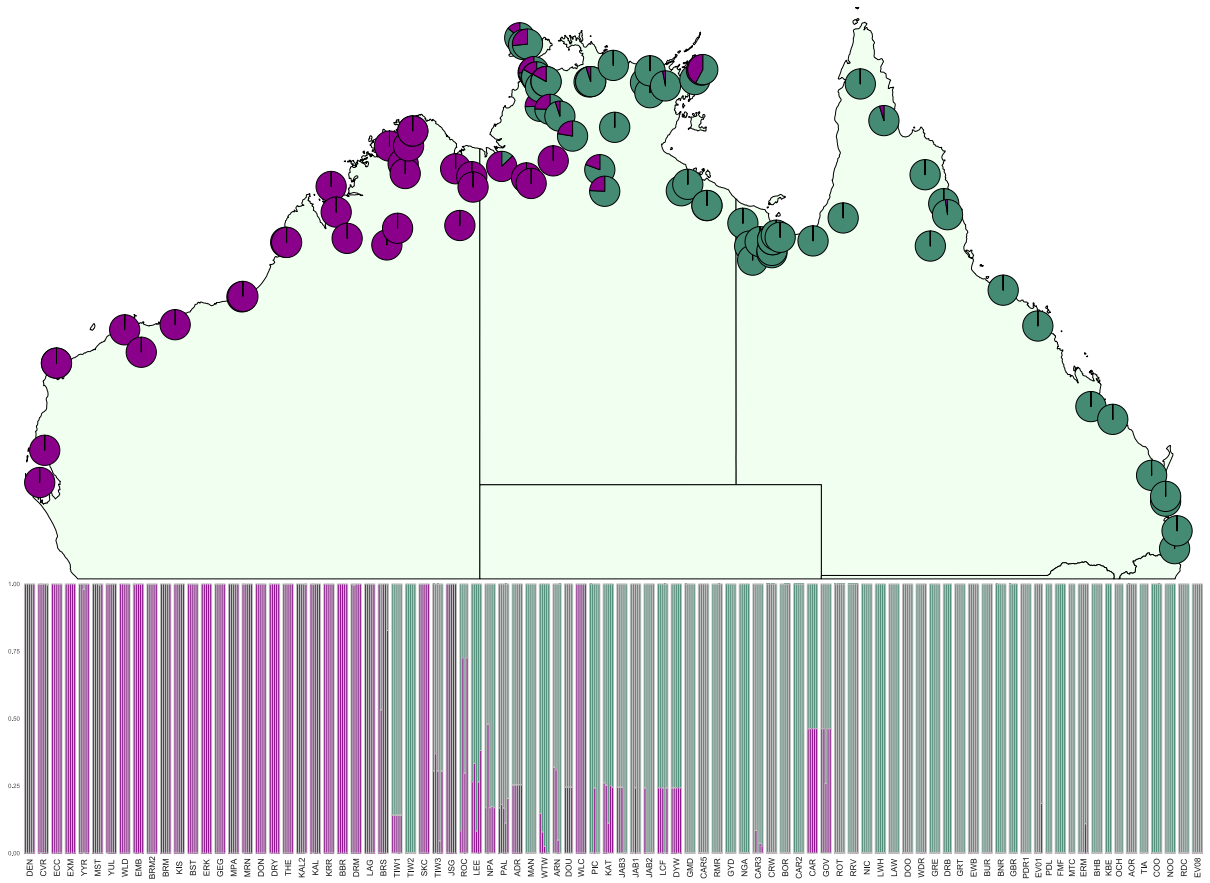


Fig. 8 Genetic clustering results from Structure analysis for the Ecuador genetic entity sites of *Passiflora foetida*. Each individual within a site is represented by a vertical bar which is apportioned into its membership to each of the identified genetic clusters

that facilitate survival and expansion of *P. foetida* in Australia under past and present conditions where it is found. Dominance of a particular weed lineage may result from a combination of biological and ecological advantages and successful traits may change through time (Baker 1974; Kempel et al. 2013; Gioria et al. 2023). These include higher fitness due to adaptive genetic traits, resistance to applied management or environmental stressors, and greater tolerance to local conditions (Kuester et al. 2014; Clements and Jones 2021; Hulme and Liu 2022). Traits such as phenotypic plasticity, competitive ability, high fecundity, efficient dispersal, and clonal reproduction can further enhance its success (Kuester et al. 2014; Clements and Jones 2021; Gioria et al. 2023).

Several sites (PDR2, KAR, MBR, MAP, CRY, see Supplementary Information for details) all in Queensland were found to have multiple genetic entities present, increasing the chance of hybridisation. There were two sites (OCH and EV01, both in QLD) with individuals of the Brazil and Ecuador genetic entity present, but only a single F1 hybrid with putative parents from the Brazil and Ecuador genetic entities was identified, indicating that hybridisation among these genetic entities is possibly limited. The low detection of hybrids between the Ecuador and Brazil genetic entities, however, does not necessarily mean that there is no cross pollination occurring, rather it may be a result of putative hybrids being less fit in the environment and not surviving to be sampled. In contrast, there were thirteen sites (ten in Queensland (CRY, MBR, PDL, PDR2, MTC, KAR, KBE, TIA, MAP, DRB, GBR) and three in Northern Territory (ARN, DOU, ROC)) that had F1, F2 hybrids or F1 backcross individuals with putative parents from the Caribbean and Ecuador genetic entities, although

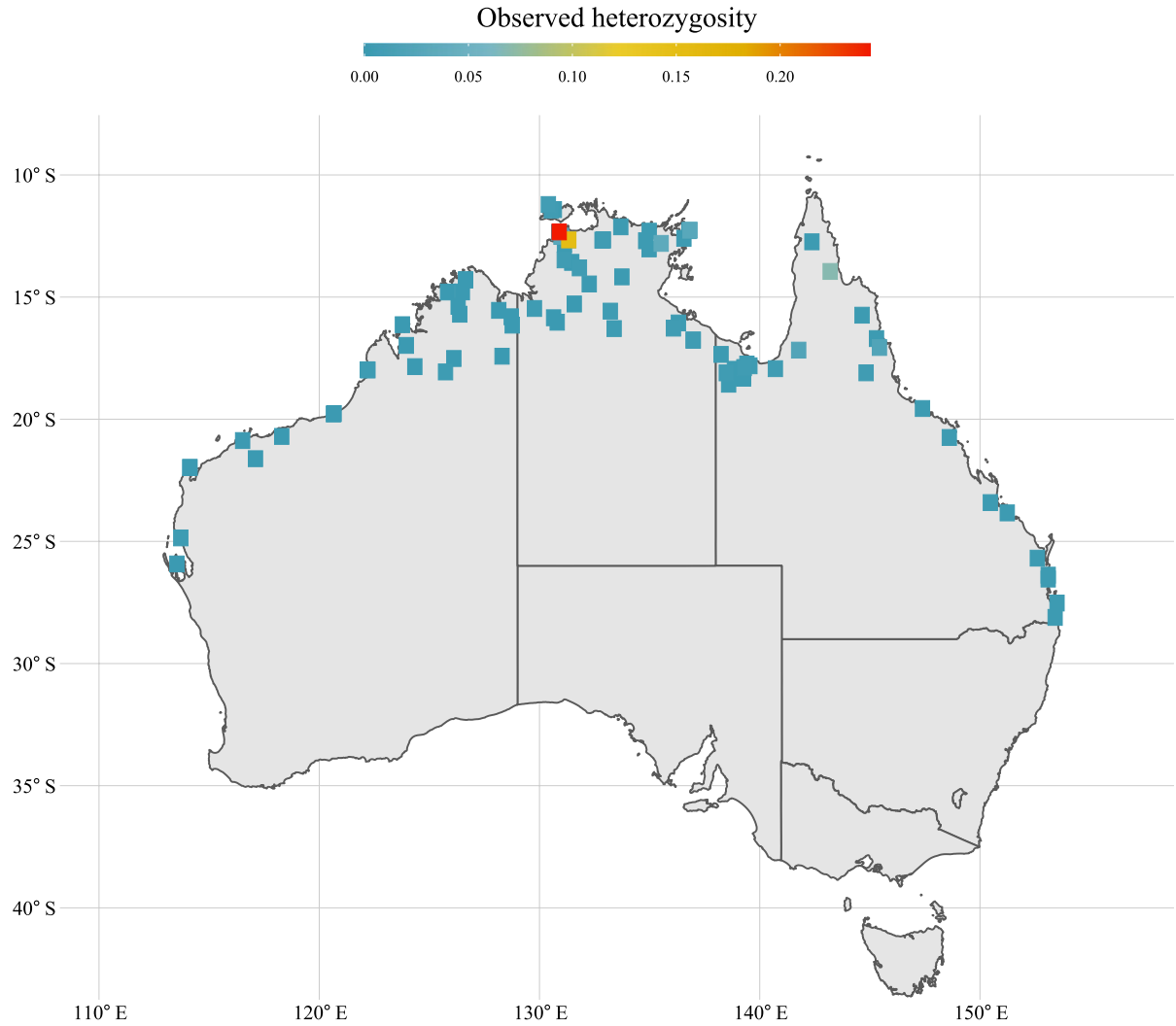


Fig. 9 *Passiflora foetida* Ecuador genetic entity observed heterozygosity values for each site, plotted at geographic location of sampled site. Blue indicates a low heterozygosity and red indicated highest observed heterozygosity

there were no sites sampled with individuals of both these genetic entities present together. This finding suggested that hybridisation may have occurred in the past in these sites or that hybridisation is occurring in non-sampled sites where individuals of both genetic entities are sympatric within the region and that hybrids have spread from these sites, or that pure plants of either genetic entity were not sampled even though they may be present at the site. Previous phylogenetic analysis has shown that the Caribbean and Ecuador genetic entities are more closely related than Ecuador and Brazil genetic entities (Hopley et al. 2021), therefore mixing between the Caribbean and Ecuador genetic entities is consistent with this closer genetic relatedness. Our results demonstrate that hybridisation is occurring, yet relatively few occurrences of hybridisation were detected in our samples, and these were quite localised in their occurrence to areas where the Ecuador and Caribbean genetic entities were located in Queensland and near Darwin. This likely reflects the more limited expansion of Caribbean and Brazil genetic entities (see below) and that the hybrids do not present increased fitness compared to individuals from the dominant Ecuador genetic entity. While hybridisation has been found to increase fitness leading to opportunities for expansion

of invasions (Buhk and Thielsch 2015; Daehler and Strong 1997; Hovick and Whitney 2014), this is not always the case. For example, admixture did not increase invasiveness in *Pinus taeda*, which was found to be driven by provenance-by-environment interactions (Zenni et al. 2014).

Heterozygosity was found to be low in sites that were only represented by the dominant Ecuador genetic entity, suggesting a low number of individuals forming the initial introduction. Introductions of species to new areas often involve limited propagules leading to founder effects that produce bottlenecks reducing genetic variation (Lawson Handley et al. 2011), while multiple introductions can alleviate founder effects and increase genetic variation (Dlugosh and Hays 2008; Petit et al. 2004). In the Ecuador genetic entity there were two sites, in the Northern Territory near Darwin, with slightly higher heterozygosity levels, and this may be a sign that there were possibly multiple introduction events for this entity that have mixed in this area. The earliest record of *P. foetida* in Australia was at a Sydney flower show in 1854 (Anon 1854), while formal records of introduction to Northern Territory date to about 1880, with its invasiveness in the Darwin area at Fannie Bay raising concern by 1891 (Holtze 1891). Given the lack of diversity in the Ecuador genetic entity elsewhere in Australia, it is likely that the localised higher diversity may have arisen through an additional introduction event. There is evidence that successful invaders with multiple introductions may take time to mix (Dlugosch and Parker 2008). In the case of the higher localised diversity in Northern Territory, the increased diversity found in those two sites is not present in other nearby sites, indicating limited gene flow among sites. The presence of sleeper diversity (reservoirs of diversity that may fuel future invasiveness, especially if selection pressures change (e.g. climate change)) has the potential over time to produce novel diversity that may be better adapted and more invasive, and these sites would be a target for removal to reduce any future increased adaptive potential of the species (Dlugosh and Parker 2008).

Our nuclear genomic analysis of the non-native range of *P. foetida* in Australia demonstrates that it has predominantly to been driven by expansion of a single entity with very low levels of diversity. Across the recent expansion of the 2000 km range in Western Australia, there is limited variation within or between sites. Introductions frequently create a genetic bottleneck leading to low diversity, yet this may not be a limiting factor in expansion of an invasive species as has been observed in other invasions characterised by low diversity. For example, *Arctotheca populifolia* is native to South Africa, and has been introduced in Australia where there has been a high loss of diversity in the non-native range but rapid morphological change in non-native sites (Buswell et al. 2011; Rollins et al. 2013). Similarly, *Phyla canescens* introduced to eastern Australia and southern France from its native range in South America was found to undergo rapid selection driven evolution and significant reduction in diversity after introduction (Xu et al. 2015). In addition to colonisation despite low diversity, it is also possible that within the initial introduced diversity in a species, there is a highly preadapted genotype that will become invasive, or that rapid adaptation may occur in the non-native range as local adaptation can evolve rapidly, alleviating environmental restrictions to colonisation (Colautti with and Barrett 2013; Sultan et al. 2013; Zenni et al. 2014). For example, analysis of the non-native *Polygonum cespitosum* in North America found a subset of genotypes with rapid and high germination and significantly greater fitness that was expressed in both favourable and stressful conditions (Matesanz and Sultan 2013). At this point it is not possible to determine whether the expansion of *P. foetida* in Australia is occurring through introduction by a preadapted genotype or through rapid adaptation after introduction. Regardless, the colonisation in eastern Australia and the recent expansion across Western Australia is occurring with very low diversity and very high fitness, suggesting a genotype with broad tolerances that can survive across a range of environmental conditions (Webber et al. 2014, 2016).

In *P. foetida*, this combination of low genetic diversity with high fitness across the non-native range presents both a challenge and an opportunity for with mitigating the impacts of this invasive weed. The capacity for an entity with such low genetic diversity to retain high fitness over the broad range of ecosystems and climates covered by the Australian distribution of the Ecuador genetic entity presents challenges for preventing spread. Yet, the low genetic variation present in *P. foetida* across the Australian range improves the chances of developing a classical biocontrol solution to target this

genotype (Burdon and Marshall 1981; Müller-Schärer and Schaffner 2008). Moreover, it enables a refined search for potential biocontrol agents in the native range by targeting searches in regions with the closest affinity to the dominant genetic variant (Lawson Handley et al. 2011). It also enables proactive testing of whether there is variable efficacy of candidate biocontrol agents on the hybrid genotypes which may limit the potential of the control agent (Garcia-Rossi et al. 2003). The lack of expansion of the two other genetic entities of *P. foetida* that are currently restricted to Queensland and New South Wales reduces the complexity of a biocontrol response. Best practice management, however, should seek to restrict the movement of these genetic entities between states or regions, even if the taxon is present in those areas, to prevent the mixing of entities that could potentially lead to an even fitter and more invasive genotype. As conditions vary through time, successful invasion is influenced by new hybridisation or admixture opportunities that create novel adaptive evolutionary combinations (Gioria et al. 2023).

Chloroplast genome analysis is particularly useful for clarifying the phylogenetic relationship of invasive weeds to native congeners. It also helps to identify source location, both of which are important for assessing biocontrol options. In contrast, nuclear genome analysis offers a more detailed examination of genetic diversity and distribution, while revealing potential hybridisation events that could shape the weed's evolutionary trajectory and influence management strategies. Our study has demonstrated the insights nuclear genomic analysis can provide for identification of introduction history and expansion in a widespread non-native invasive species. This insight has provided key information that can be used to refine management of *P. foetida* in Australia, particularly in regard to pursuing biocontrol solutions. Further work would benefit from more in-depth genomic analyses to investigate the development of the adaptive capacity of the dominant Ecuador genetic entity and the potential genomic basis of its invasive traits.

Data repositories

The datasets generated for this study can be found at FigShare in the *Passiflora* genomic datasets repository (https://figshare.com/s/ad0138985f6ef24307fa).

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Author's contributions MB, BW, SR and LM developed the project. TH and MB designed the study. All genetic data analysis was done by TH. TH drafted the paper with the input from MB and BW, all authors contributed to revision of the manuscript.

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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