The population structure of invasive *Lantana camara* is shaped by its mating system

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Abstract

Over the last century, invasive species have emerged as an important driver of global biodiversity loss. Many invasive species have low genetic diversity in the invaded habitats, owing to the demographic bottleneck during introduction. *Lantana camara* is one of the hundred most problematic invasive species globally. Despite its ecological importance in many countries, our understanding of the genetic diversity patterns of this plant remains poor. Previous studies hypothesize that invasive *L. camara* is a species complex with a hybrid origin, but this remains untested. We investigated the population genetic patterns of this invasive species by sampling 359 plants that represented a spectrum of flower colour variants across 36 locations, spanning most of the biogeographic regions across India. Analyses of the population structure using 19,008 SNPs revealed that *L. camara* in India exhibits a strong genetic structure. Interestingly, the structuring pattern does not exhibit a strong correlation with geography. In the structure analysis, individuals with similar flower colours clustered together regardless of their location of origin. The genetic distance between most of the individuals was low, indicating the absence of multiple species. A high inbreeding coefficient and a low proportion of heterozygous sites observed suggested that the strong structure could be due to self-fertilization. Thus we infer that *L. camara* exists as homozygous inbred lines formed by self-fertilization and that these inbred lines could be associated with distinct flower colours. Together, this would explain the correlation between flower colour and genetic structure, and the lack of geographic structure. These results refute the argument that *L. camara* is a species complex and emphasize the importance of the mating system in shaping the patterns of diversity in this invasive species. Our findings highlight a hitherto unknown role for mating

systems in invasive species, furthering our understanding of evolution in invasive species.

1. Introduction

Invasive species are one of the major causes of ongoing biodiversity loss and extinctions in the Anthropocene (Linders et al., 2019; Mollot et al., 2017). Understanding the ecological and evolutionary underpinnings of invasion success is critical to controlling the emergence of new invasive species. Evolutionary and population genetic theory suggests that among other factors, genetic variation is critical to demographic success and range expansion (Ørsted et al., 2019). Populations that have undergone a demographic bottleneck are expected to have low genetic variation, which can negatively impact their ability to survive and adapt (Olazcuaga et al., 2023).

Invasive species typically undergo demographic bottlenecks during colonization (Alves et al., 2022). Low propagule pressure (the number of individuals introduced) leads to low effective population size. Consequently, invasive populations are established under conditions of limited genetic variation (Dlugosch & Parker, 2008; Simberloff, 2009). Despite the theoretical expectation of low genetic variation, invasive populations paradoxically demonstrate the ability to adapt, thrive and reproduce in large numbers in these novel habitats. This phenomenon is called the genetic paradox of biological invasions(Estoup et al., 2016). While extensively debated, some studies support the presence of such low genetic variation (Alves et al., 2022) while others contradict it (Bastien Lavergne & Molofsky, 2007; Zhang et al., 2021). The inherent complexities of human-mediated introduction like the choice of

source population, number of introductions, artificial hybridizations etc. along with evolutionary forces make the patterns of genetic variation in invasive populations complicated (Roman & Darling, 2007). Several factors such as propagule pressure, hybridizations, gene flow, mating system etc. play an important role in determining the amount of genetic variation in invasive populations (Jaspers et al., 2021).

The introduction of many individuals either through single or multiple events can bring high variation into the novel environment (Bastien Lavergne & Molofsky, 2007). The source populations from which these individuals originate can influence the patterns of genetic diversity (Ryan et al., 2019) in new populations. Gene flow between multiple invasive populations can homogenize genetic variation (Vallejo-Marín et al., 2021). Intraspecific hybridizations between genetically distinct individuals can lead to the formation of new genotypes with novel allelic combinations, while hybridization with native species can aid in rapid adaptation (Blair & Hufbauer, 2010; Mesgarana et al., 2016). In plant populations, mating systems play a role in determining the pattern of genetic diversity (Hamrick et al., 1992; Ness et al., 2010; Schoen & Brown, 1991). Theoretically, cross-fertilizing species have high heterozygosity, and hence high genetic variation (Koelling et al., 2011). Conversely, with self-fertilization heterozygosity decreases by 50% every generation (Hedrick 2011). This leads to high genome-wide homozygosity and individuals exist as homozygous inbred lines (Guo et al., 2008; Pérez De La Vega & Garda, 1997). In self-fertilizing species, neutral diversity is low due to low effective population size (Foxe et al., 2009; Guo et al., 2008; Koelling et al., 2011), and it results in high genetic drift. The combination of low gene flow, high drift and high homozygosity leads to a strong genetic structure in self-fertilizing species compared to cross-

fertilizing species (Edwards et al., 2019; Koelling et al., 2011; Mairal et al., 2023). While mating systems play an important role in determining genetic diversity, to the best of our knowledge, their role in invasive species has not been specifically investigated.

Here we present the genetic diversity patterns of the globally invasive plant species, *Lantana camara* (Lantana hereafter) in India. Lantana is a perennial shrub native to Central and South America. During the colonial era, this species was introduced into many countries across the globe, like India, Australia and South Africa as a garden plant (Kannan et al., 2013). Currently, it is one of the most important invasive species in India with a significant impact on the native ecosystems. On average, Lantana threatens almost 44 per cent of the forest areas in India (Mungi et al., 2020). In the Bandipur tiger reserve in southern India, Lantana occupies at least 40 per cent of the land area (R et al., 2016). Unlike many invasive species, Lantana exhibits extensive phenotypic variation in India (Negi, Sharma, & Vishvakarma, 2019), with the most striking being the variation in flower colour. By 1900, approximately 16 species of the genus Lantana were reported in India, potentially suggesting multiple introductions. The taxonomy of the genus Lantana is complicated due to the presence of polyphyletic groups (Lu-Irving et al., 2021). In the taxonomy, many flower colour variants of Lantana are classified as distinct species (Sanders, 2006). However, genetic validation of this classification, focusing on different flower colour variants has not been done. It is possible that active hybridization to produce new hybrids took place in botanical gardens (Goyal & Sharma, 2015a; Urban et al., 2011). Previous studies have hypothesized that invasive Lantana is a species complex, potentially formed from such hybridization

events (Goyal & Sharma, 2015b; Sanders, 2006). Variation in Lantana flower colour lends support to the species complex hypothesis. As a result, the invasive Lantana is sometimes referred to as *Lantana camara* sensu lato (Goyal & Sharma, 2015c). Detailed genetic studies are important in checking this hypothesis and characterising different species of this genus.

Despite its status as one of the most pervasive invasive species globally, our understanding of its biology and genetics remains limited. It is further complicated by uncertainties regarding its species identity. Investigating the genetic diversity patterns of Lantana presents an opportunity to improve our understanding regarding the uncertainties about the species identity, as well as the genetic paradox of biological invasions. This can help in improving our understanding of the taxonomy of Lantana itself. A previous population genetic study using microsatellite markers suggests that Lantana populations in India are genetically homogeneous (Ray & Quader, 2014). However, as discussed earlier, its ecological and demographic success is very high along with the high phenotypic variation. We use thousands of genome-wide Single Nucleotide Polymorphism (SNP) markers and genetic simulations to investigate the patterns of genetic diversity, spatial genetic structure and the factors shaping these patterns in Lantana populations in India. We use India as an example of a large, ecologically diverse landmass where Lantana has been highly successful. More specifically, we investigate i) the genetic diversity and population structure of Lantana populations in India, and ii) the evolutionary forces shaping the genetic diversity patterns of Lantana.

2. Material and Methods

2.1 Study system

Lantana camara is considered to be one of the hundred most invasive species in the world (IUCN 2000). It was introduced across the globe as a garden plant because of its strikingly attractive flowers. The earliest recorded presence of Lantana in India comes from the British botanical garden in Kolkata in 1807 (Kannan et al., 2013). Currently, it is widely distributed in India occupying almost every terrestrial habitat (Mungi et al., 2020). In India, Lantana exhibits extensive phenotypic variation with the most remarkable being the variation in the flower colour (Negi, Sharma, Vishvakarma, et al., 2019). Lantana produces umbellate inflorescence with younger flowers in the centre and older ones in the periphery. The colour of the flowers may change post-pollination, thus a single inflorescence can have flowers of different colours (Negi, Sharma, & Vishvakarma, 2019). Yellow-pink (yellow young flowers in the centre of the inflorescence and older pink flowers in the periphery), White-pink and Orange (flowers maintain more or less the same colour) flower colour types are commonly observed in India (Fig. 1b). Flower colours like reddish-pink, yellow-orange and pink (Fig. 1b) are relatively uncommon. A single location can have multiple of these flower colour variants growing together next to each other.

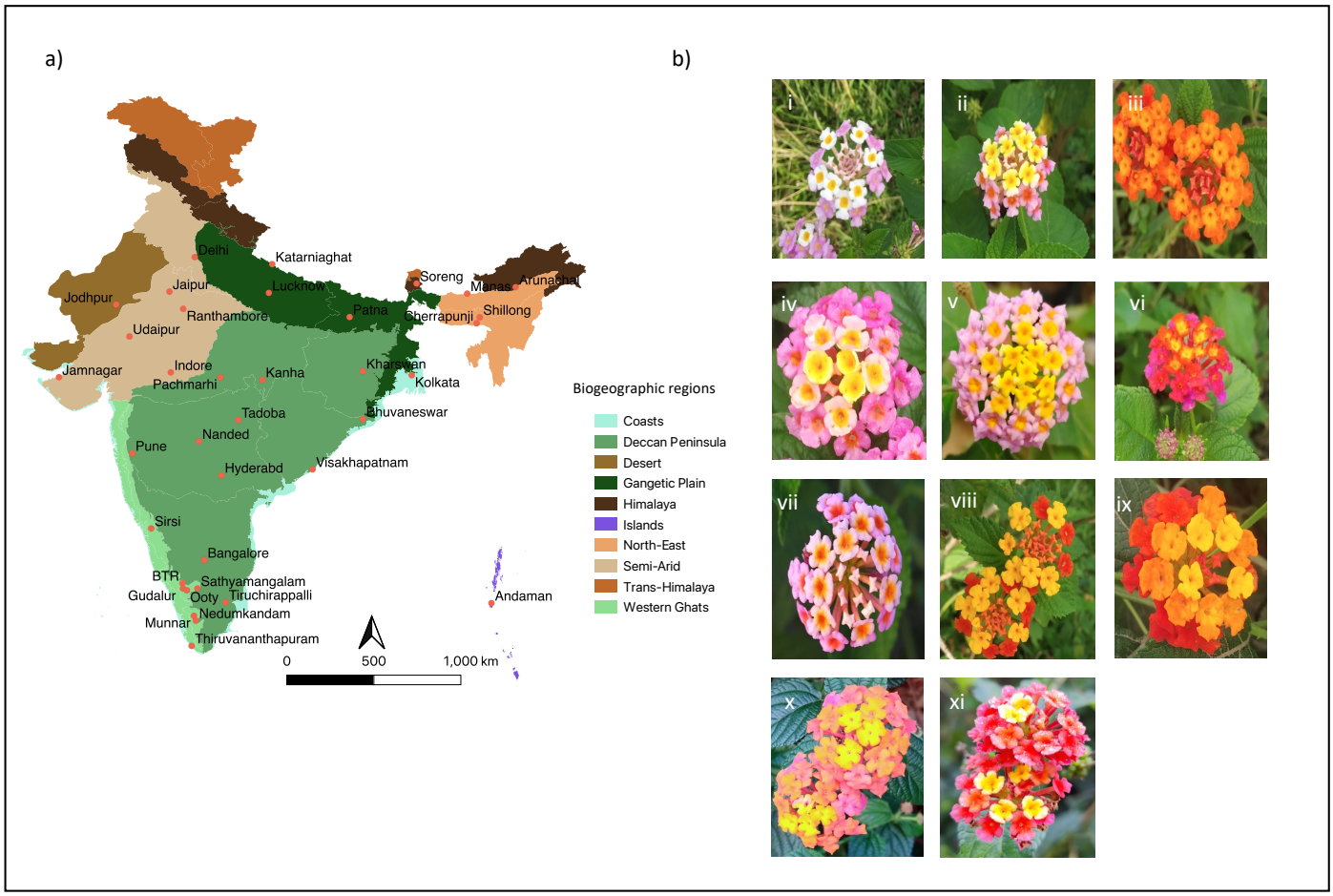

Figure 1 Sampling locations (a) of Lantana across different biogeographic regions in India Flower colour variation (b) of Lantana. i- White-pink, ii- Yellow-pink, iii- orange, iv- Yellow-pink-b, v - Yellow-pin-c, vi - Reddish-pink, vii- pink, viii- yellow-orange, ix - yellow-orange-b, x – Yellow-dark-pink a, xi - Yellow-dark-pink b

2.2 Sampling locations

Lantana plant samples were collected between the years 2020 and 2023. Plants were collected from 36 locations across the country, representing various bioclimatic regions (Fig. 1a, Supplementary Table 1). Wild-growing plant saplings were collected and planted in the greenhouse at the National Center for Biological Sciences, Bengaluru. From each location, a few plants that represented different flower colour types were selected randomly for the genomic analysis. We received silica gel-dried leaf samples from four locations which were also included in the study. Whenever possible, we have noted the flower colour during collection, or in the

182 greenhouse—however, the exact flower colour of 59 plants that died before flowering
183 is unknown.
184
185 2.3 DNA extraction and sequencing library preparation
186 Two to three fresh leaves were collected from each plant for DNA extraction.
187 Leaves were crushed using liquid nitrogen in a mortar and pestle. A Qiagen DNeasy
188 plant pro kit was used for the extractions, following the manufacturer's instructions.
189 DNA was quantified using a Qubit fluorometer. 199 µl Qubit buffer and 1 µl dye were
190 mixed and 199 µl of this mix was used with 1µl DNA to check the concentrations.
191 Extracted DNA was stored at -20 degrees Celsius. Double-digest Restriction-site-
192 associated DNA (ddRAD) libraries were prepared using the modified protocol by
193 Tyagi et al 2024. Briefly, genomic DNA was digested using two restriction enzymes;
194 SphI a six-base pair and MlucI a four-base pair cutter. Adapters specifically designed
195 for SphI and MlucI are ligated to the cut ends. Unbound adapters were removed
196 using magnetic bead-based cleaning, where 0.5X beads were used to remove
197 fragments shorter than 50 base pairs. Individual specific index combinations were
198 ligated to each sample using PCR and amplification was carried out. The PCR
199 products were dual size selected for a target library size of 200 to 500 bp using
200 magnetic beads. Library quality was evaluated using a TapeStation automated
201 electrophoresis system. All the samples were pooled to get a 2nM library and the
202 final library was sequenced in HiSeq2500 and NovaSeq6000 platforms.
203
204 2.4 Variant calling and filtering
205 Raw reads were demultiplexed and barcodes were trimmed using a custom
206 script. Raw reads were quality-controlled using Trimmonatic - v.0.33.0 (Bolger et al.,

207 2014). Reads with an average quality lower than 30 and reads shorter than 30 bp
208 were excluded. Trimmed reads were aligned to a draft reference genome of *L.*
209 *camara* (Joshi et al, 2022) using BWA-MEM (Li & Durbin, 2009) with default settings.
210 We used Freebayes (Garrison & Marth, 2012) to call variants using the default
211 settings, which were filtered using VCFtools (Danecek et al., 2011) to retain only
212 high-quality SNPs. The filtering was done in the following order: biallelic SNPs were
213 retained, SNPs with a minimum depth of 10 and a maximum depth of 500 were
214 retained. Sites with a minimum genotyping quality of 30 and a minor allele count of at
215 least three were kept. Individuals with more than 90% missing data were removed.
216 SNPs that are not in Hardy-Weinberg equilibrium were removed. Finally, SNPs
217 present in at least 90 per cent of the individuals were retained. The filtered VCF was
218 used for all further analyses.
219
220 2.5 Population structure and genetic diversity estimations
221 We used a Bayesian clustering approach (ADMIXTURE) and a multivariate
222 approach (Principal Component Analysis) to understand the genetic structuring of
223 Lantana. Principal Component Analysis (PCA) was carried out using PLINK (Purcell
224 et al., 2007). Genetic population structuring was investigated using the model-based
225 clustering algorithm ADMIXTURE (Alexander et al., 2009), with K values ranging
226 from 2 to 17. We used Evanno's delta K method (Evanno et al., 2005) implemented
227 in the web server CLUMPAK (Kopelman et al., 2015) to find the optimum K.
228 CLUMPAK was used to plot the admixture proportions as well. The structure plot was
229 rearranged for easy visualization. Inbreeding coefficients and heterozygosity were
230 estimated using the R package Adegenet (v2.1.10) (Jombart, 2008). F_{ST} was
231 estimated using Weir and Cockerham's method implemented in VCFtools (Danecek

et al., 2011). Adegenet (v2.1.10) was used to test for isolation by distance. Nei's genetic distance was calculated using the StAMPP package (Pembleton et al., 2013) in R. A phylogenetic network was generated using the r package StAMPP and the SplitsTree4 (Huson, 1997).

2.6 Genetic simulations

We used SLiM (Haller & Messer, 2019), a forward-in-time, individual-based simulation program to understand the importance of mating systems on the pattern of genetic diversity in invasive plant species. Populations analogous to both native and invasive populations were simulated with different mating systems. All the individuals in the simulations were diploid hermaphrodites, with 10 chromosomes each with 1,00,000 bps. The mutation rate and the recombination rate were assumed to be 10^{-8} and 10^{-7}respectively (Igor Kovalchuk, 2000), which is the general mutation and recombination rate for plants. Generations were assumed to be non-overlapping. Scenarios with different mating systems having varying levels of self-fertilization (zero - complete crossing, 25, 50, 75 -mixed-mating and 100- complete selfing) were simulated. A schematic representation of the demographic changes during the simulation is shown in Figure 2. The simulation started with a single population of 100 genetically identical individuals, which grew exponentially (growth rate=1.05) until they reached a carrying capacity of 10,000 individuals. This carrying capacity was decided, to reduce the computational complexity. In the burn-in phase, the individuals evolve under these conditions for 20,000 years/generations. In the 20,000th year, two new populations were created by individuals migrating from the initial simulated population (assumed to be the native population). The number of founding individuals (in this case propagule pressure) was either 10, 100 or 1000. These populations

grew exponentially to a carrying capacity of 10,000 with the same growth rate. The population evolved till the year 20,200 and thus 200 generations after invasion is simulated. The population level heterozygosity, nucleotide diversity and F_{ST} between populations were measured at the end of the 20th and 200th generations. For randomly selected 50 individuals from each population, VCF files with SNP information were created at the 20,200th generation.

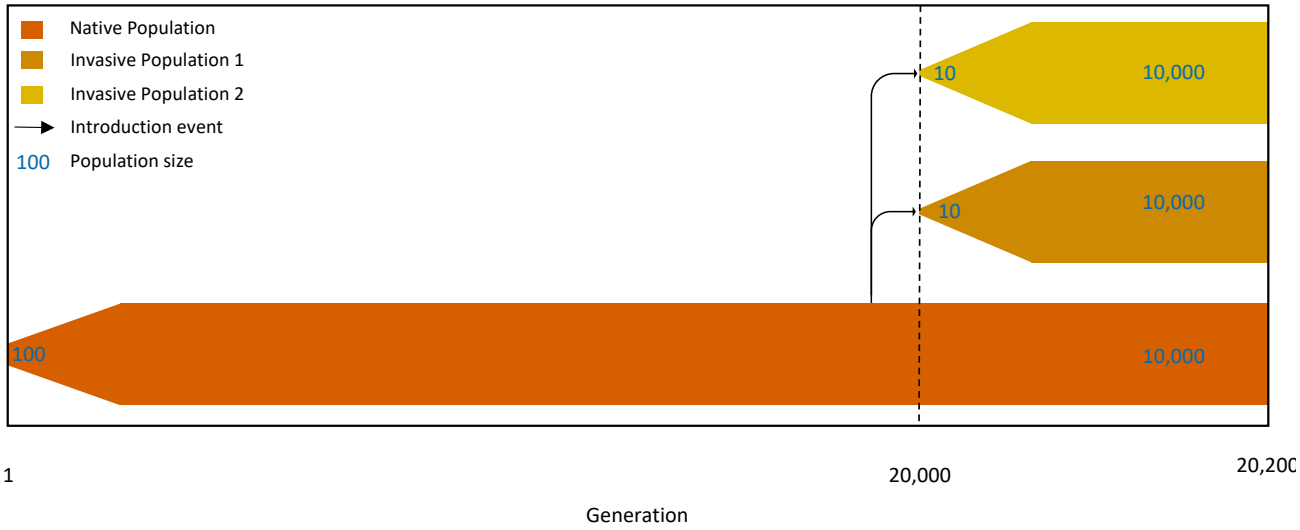

Figure 2 Schematic of the SLiM simulations. In generation one, a single population is formed with 100 individuals. It exponentially grows and reaches a carrying capacity of 10,000. At generation 20,000 two new invasive populations are formed, founded by 10 individuals each. Further, all three populations evolve for 200 more years.

3 Results

3.1 Invasive Lantana populations in India show strong genetic structure

Using ddRAD sequencing, we obtained 19,008 SNP markers for 359 Lantana individuals from different regions across India. This SNP dataset was utilised to assess the genetic differentiation in Lantana through three different analyses: Structure, Principal component analyses and fixation index. Structure analyses using the ADMIXTURE package revealed strong genetic structure in the Indian Lantana

populations (Fig. 3a). The optimum number of Hardy-Weinberg populations was between four and eleven (Supplementary Figure 1). At K=4, which had the highest support for the optimum number of clusters, the geographic origin did not dictate the genetic structuring. Despite belonging to the same geographic location, individuals were assigned across different genetic clusters. At K=3, nine individuals from North-Eastern India clustered together and maintained a distinctive identity at higher K as well. Many individuals were admixed. K=8 and 11 had the second and third highest log likelihood values for the optimum K.

The principal component analysis results corroborated the findings from the admixture analyses (Fig. 3b and c). In the PCA encompassing all 359 samples (Fig.3b), PC 1 explained 44.8% of the variation and PC 2 explained 6.4% of the total variation. Nine samples from North-eastern India formed a distinct cluster separate from the rest of the samples in the PC1 axis (Fig. 3b). To explore the structuring pattern within the remaining samples, a separate analysis excluding these nine individuals was carried out (Fig. 3c). In this analysis, PC 1 explained 16.2% of the variation and PC 2 explained 11% of the variation. In the PCA, samples were coloured based on the geographic location from south to north of India (brown to green respectively). Individuals from geographically distant locations were clustering together while those from the same geographic area were assigned to different clusters in many locations, reinforcing the absence of a strong geography-based pattern. A flower colour-based clustering pattern was evident in the PCA with samples colour-coded according to the flower colour (Supplementary Figure 2).

The isolation by distance analysis using the Mantel test (Fig. 3d) revealed a weak correlation between genetic distance and geographic distance (Mantel r = 0.039, p-value = 0.075), indicating that geography is not the major factor influencing the structuring pattern. The fixation index (F_{ST}) between most of the population was low (Supplementary Table 2). Arunachal Pradesh (in north-eastern India) samples showed high F_{ST} with many populations (0.46 to 0.54) (Supplementary Table 2).

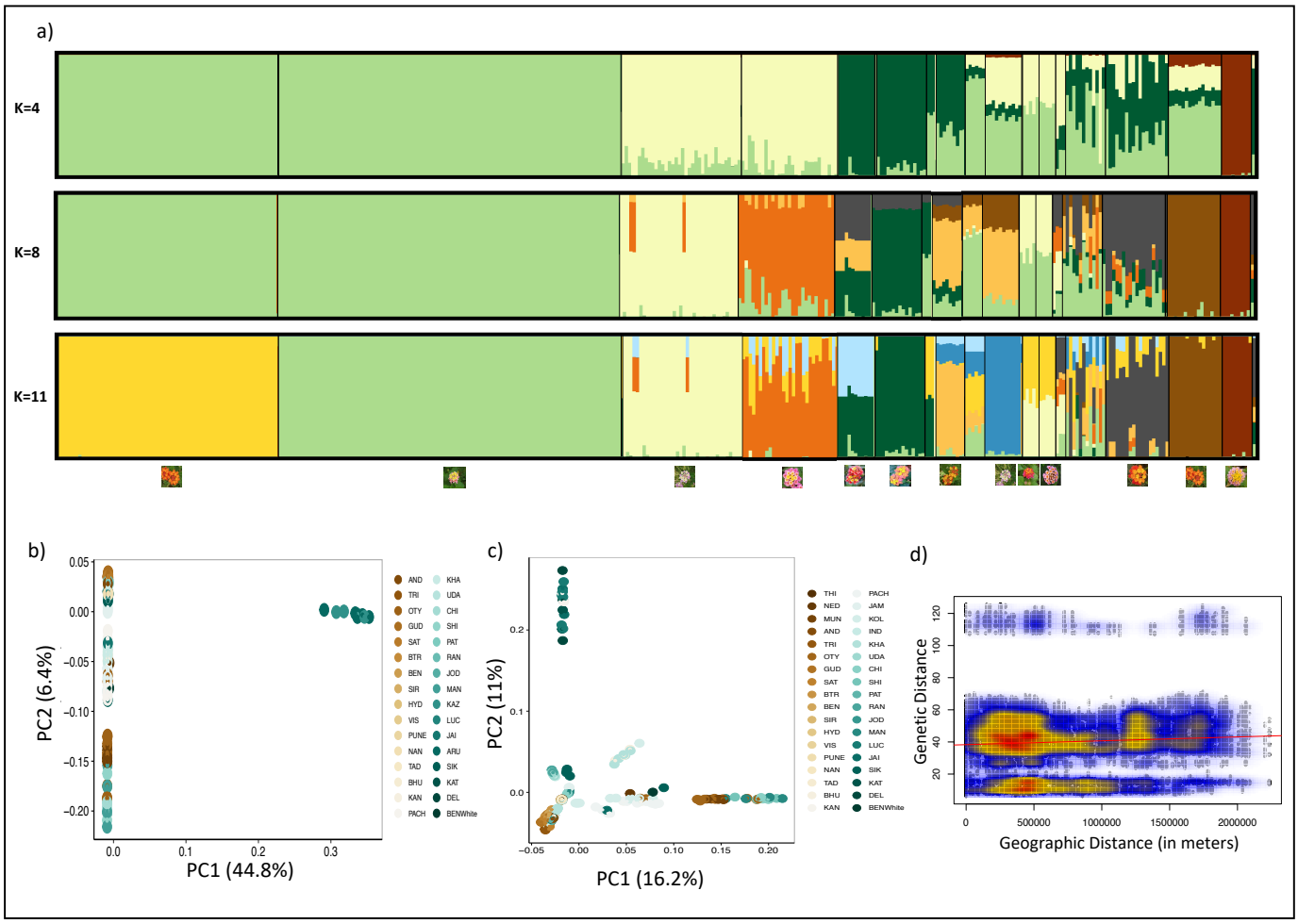

Figure 3 Population structure of Lantana in India. a) Genetic ancestry assignment based on the programme ADMIXTURE. Ancestry fractions assuming four, eight and eleven ancestral populations are given. Clusters are arranged based on the flower colour variants b) PCA of all 359 samples c) PCA of all samples except nine northeast Indian samples. Individuals are coloured based on their geographic locations from north to south of India d) Isolation by distance showing a weak correlation between genetic distance and geographic distance

3.2 Genetic population structuring in Lantana is associated with flower colour

316 In the Admixture analysis, the clusters closely aligned with distinct flower colour
317 variants of Lantana. At K=4, yellow-pink and some of the orange-flowered Lantana
318 clustered together, while a separate cluster comprised pink and some of the white-
319 pink individuals (Fig. 3a) . A third cluster was formed by dark-pink-coloured plants
320 from Ooty (Southern India) and North-east India. Nine individuals from northeast
321 India formed a fourth cluster. Other flower colour variants were admixed.
322 Interestingly, at K=11, a pronounced flower colour-based clustering pattern emerged,
323 with distinct clusters formed by yellow-pink, pink, reddish-pink, dark pink and yellow-
324 orange individuals, while both orange and white-pink Lantana each formed two
325 separate clusters. In the PCA, the clustering pattern often mirrored the flower colour
326 variants (Supplementary Figure 2). Yellow-pink colour variant formed a tight cluster.
327 One of the orange colour variants also showed a similar trend. In the phylogenetic
328 network generated using SplitsTree, (Fig. 4a) most of the individuals were grouped
329 according to their flower colour. The most common flower colour in the country,
330 yellow-pink, formed a single cluster in admixture analysis and in the SplitsTree
331 network. Most of the yellow-pink and orange individuals across the country had short
332 branch lengths in the phylogenetic network.
333
334 High Inbreeding and low genetic diversity characterize Lantana populations
335 Nearly all the individuals exhibited a very low proportion of heterozygous sites, with
336 less than 10% heterozygous sites (Fig. 4c). However, the nine individuals from North-
337 East India showed the highest proportion of heterozygous sites (>0.3). The
338 inbreeding coefficient of many of the individuals was extremely high, suggesting high
339 levels of self-fertilization (Fig. 4d). The Nei's genetic distance between most of the
340 Lantana individuals across the country was very low indicating the absence of

genetically distinct lineages (Fig. 4b). Even with low genetic distance, there is often strong differentiation within a location. The genetic distance was high only for the nine individuals from the northeast of India with the rest of the samples. This was reflected in the phylogenetic network, where the nine northeast individuals formed a distinct group with long branch lengths (Fig. 4a).

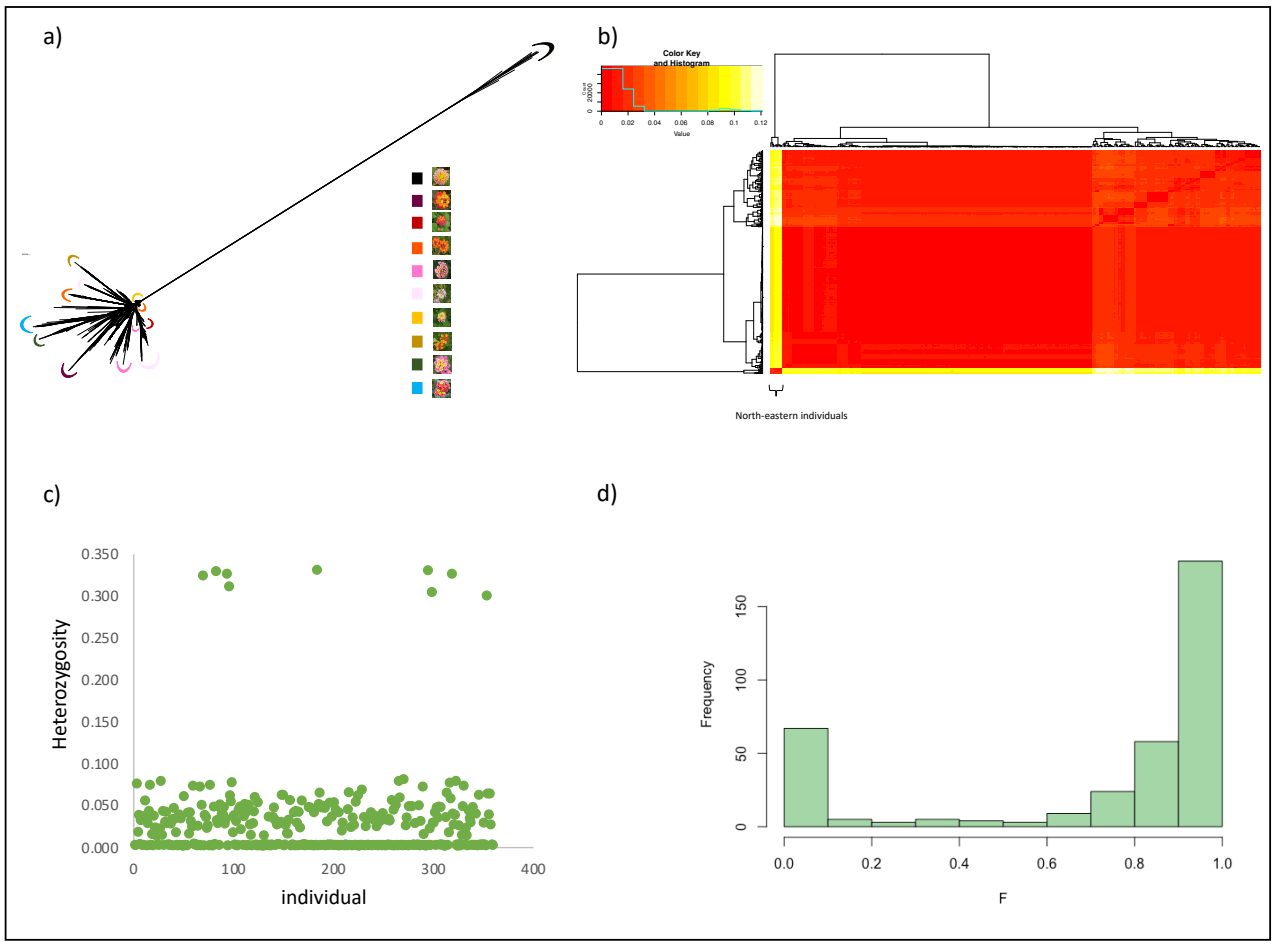

Figure 4 Signatures of high inbreeding due to self-fertilization in Lantana a) Phylogenetic network using SplitsTree4, lineages are coloured based on the flower colour b) Nei's genetic distance between all the individuals, nine northeast India samples are genetically most distinct c) Proportion of heterozygous sites per individual d) Inbreeding coefficient

3.3 Genetic diversity in invasive populations is influenced by the mating system.

To understand the influence of the mating system on genetic diversity in invasive plant species, we have carried out an individual-based genetic simulation using SLiM.

356 These simulations confirmed that the mating system strongly impacts standing
357 genetic variation within a species. Simulations of cross-fertilisation resulted in higher
358 heterozygosity and nucleotide diversity than those of self-fertilization (Fig. 5 a and b).
359 This was consistent across various propagule pressures (10, 100 and 1000)
360 simulated. The heterozygosity and nucleotide diversity were low in the simulated
361 invasive populations compared to the simulated native population (Fig. 5 a and b). An
362 increase in the propagule pressure did not substantially increase the genetic
363 diversity. Under the same propagule pressure, simulations of cross-fertilization gave
364 rise to invasive populations with high genetic diversity compared to scenarios with
365 self-fertilization. The variance in heterozygosity and nucleotide diversity was high in
366 the self-fertilizing simulation scenarios.
367
368 Mating systems had an impact on the differentiation of simulated native and invasive
369 populations. F_{ST} between simulated native and invasive populations revealed that the
370 F_{ST} value was lowest under complete cross-fertilization (Fig. 5c). The differentiation
371 increased as the percentage of self-fertilization increased. Under simulations of
372 complete self-fertilization, the variance was high and F_{ST} ranged from approximately
373 0.03 to 0.69. Whereas, in complete cross-fertilization, it ranged from 0.07 to 0.2.
374 Similarly, in simulations of cross-fertilization, the differentiation between simulated
375 invasive populations was low compared to self-fertilisation scenarios (Fig. 5d). The
376 differentiation increased as the allowed selfing percentage increased. F_{ST} ranged
377 from 0.05 to 0.98 in self-fertilizing simulation scenarios. Within each category of
378 selfing percentage, an increase in the propagule pressure reduced the differentiation.

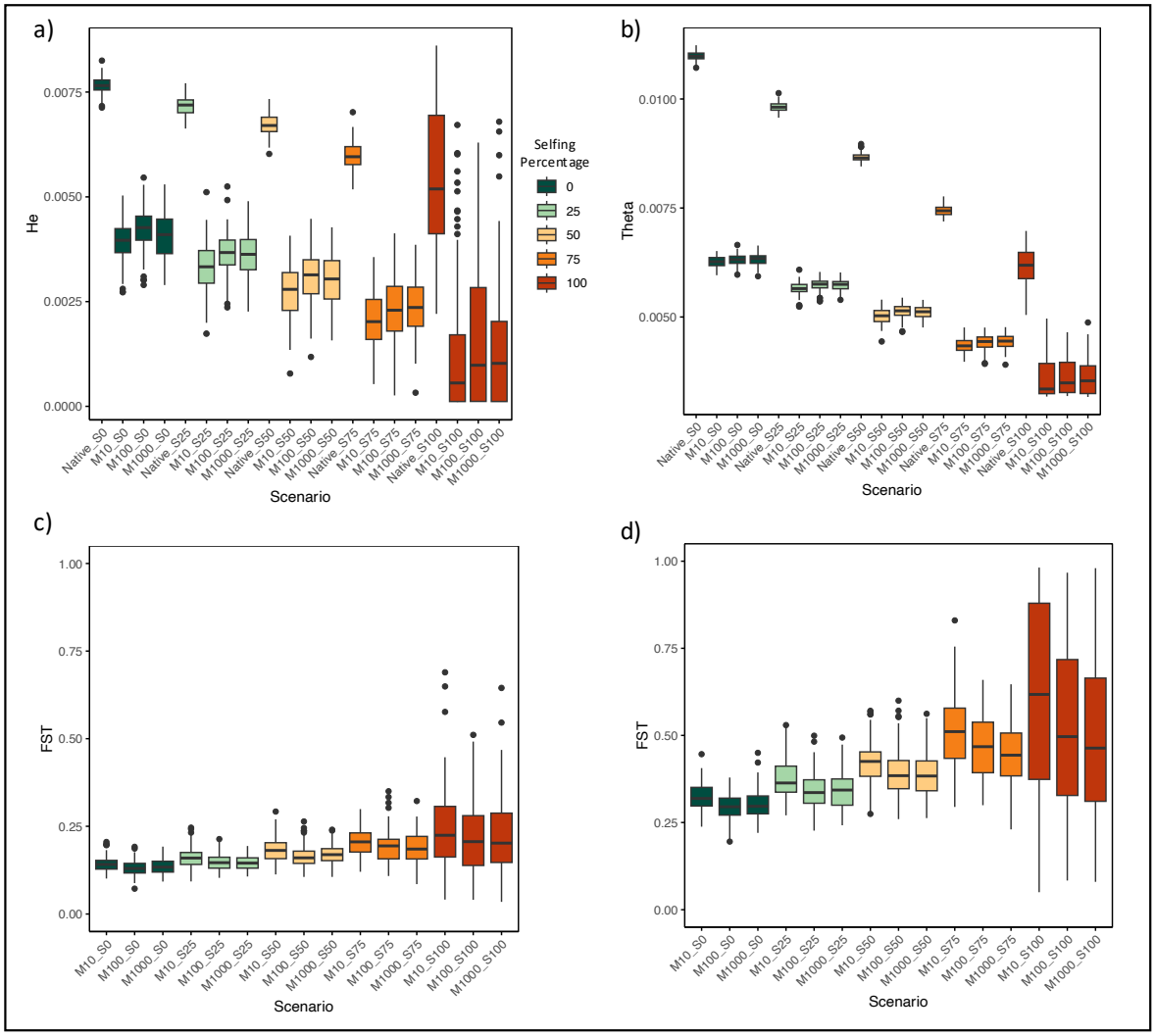

Figure 5 Individual-based genetic simulation results showing putative patterns of genetic diversity in invasive plants under different assumed mating systems and propagule pressure. Heterozygosity (a) and nucleotide diversity (b) under different mating systems in 'native' and 'invasive' populations founded by 10, 100 and 1000 individuals c) F_{ST} between 'native' and 'invasive populations' under different simulated mating systems and propagule pressure. d) F_{ST} between two simulated 'invasive populations' under different mating systems and propagule pressure.

Self-fertilization leads to strong structuring within the simulated populations. PCA using SNPs from individuals of all three populations revealed a strong genetic structure in self-fertilization scenarios (Supplementary Figure 3). Whereas, in cross-fertilization scenarios, there was a weak structure (Supplementary Figure 3). Under

selfing, individuals from the same population were assigned to distinct genetic clusters, and within a cluster, individuals from multiple populations were present.

4 Discussion

Biological invasions pose a serious global challenge, with millions of dollars spent annually on their control (IPBES, 2023). Yet, it is often difficult to control the emergence of new invasive species and their spread due to the lack of understanding of the invasion process and the factors contributing to invasion success. Critical to understanding invasion success is an understanding of standing genetic variation and population differentiation. We used genomic techniques to understand patterns of genetic diversity and differentiation in invasive Lantana populations in India. Our findings revealed that Lantana populations in India are genetically structured, but the structuring pattern was not strongly correlated with the geography. In the Admixture analysis, the genetic structure aligned with flower colour variation. Notably, many individuals exhibited a high inbreeding coefficient and a very low proportion of heterozygous sites. Genetic distance and phylogenetic network indicated that lineages are relatively similar. We suggest that the strong genetic structure despite the low genetic distance is because of the increased homozygosity due to self-fertilization. Through genetic simulations, we show that the mating system can impact genetic diversity and the structure of simulated, putatively invasive species.

4.1 Population structure

Our investigation into the genetic structure of Lantana using both Admixture and principal component analysis revealed a strong population structure. Individuals from

the same geographic location were assigned to different genetic clusters, contrary to a previous study using microsatellite markers which suggested genetic homogeneity in Lantana populations in India (Ray & Quader, 2014). SNP markers are numerous in the genome, and as a result, have higher statistical power than microsatellite markers (Zimmerman et al., 2020). We have used 19,008 SNP markers and thus we expected population structure to be better resolved.

In PCA, admixture, and phylogenetic network nine individuals from the northeast of India were genetically distinct compared to the rest of the samples. These samples exhibited high heterozygosity compared to other plants, which could explain their genetic distinctiveness. These plants also had noticeable phenotypic differences, such as a lack of thorns and dense trichomes on leaves. Further detailed analyses of these plants are required to better understand the basis of such a large genetic difference.

Many invasive species show strong genetic structure in the invaded ranges (Wang & Chen, 2017) due to multiple introductions, followed by the lack of gene flow between populations (Bastien Lavergne & Molofsky, 2007). However, in many such studies, a geography-based population structuring pattern is observed (Le Cam et al., 2020). Our genetic results corroborate the expectation of multiple introductions as suggested by the historical records on Lantana (Kannan et al., 2013). As expected with multiple introductions, we find multiple genetic clusters (across populations) and phenotypic (varied flower colours) diversity in invasive populations of Lantana in India. However, our findings are unique because, despite having multiple genetic clusters, we do not find geographic structuring.

442

443 4.2 Self-pollination leading to high homozygosity in Lantana

444 Most of the Lantana individuals in India show a high inbreeding coefficient and a low
445 proportion of heterozygous sites. In plants, high inbreeding coefficient and low
446 heterozygosity are associated with self-fertilization (Hedrick 2011). These results
447 indicate that Lantana is predominantly self-fertilizing in India and exists as
448 homozygous inbred lines. This is further supported by Structure and PCA results. In
449 many natural populations of plants, the type of mating system is shown to influence
450 the patterns of genetic diversity (Bomblies et al., 2010). Mating systems in plants
451 range from uniparental reproduction or self-fertilization to obligate cross-fertilization
452 or outcrossing (Charlesworth, 2006). Approximately 10-15% of seed plants
453 predominantly self-fertilize (Goodwillie et al., 2005). Many species exhibit mixed
454 mating systems, including a combination of both selfing and outcrossing (Whitehead
455 et al., 2018). Mating systems influence the effective population size and thus play a
456 crucial role in shaping genetic diversity within a species (Laenen et al., 2018).

457

458 In its native range, Lantana primarily relies on cross-fertilization for reproduction
459 (Barrows, 1976). However, in the introduced range, Lantana is self-compatible
460 (Goulson & Derwent, 2004; Ram & Mathur, 1984). During colonization and invasion,
461 plant species can shift mating systems from cross-fertilization to self-fertilization
462 (Petanidou et al., 2012; Willi et al., 2022). A detailed study of mating systems in
463 native and invaded ranges is required to confirm such a shift in the case of Lantana.
464 Self-fertilization is shown to increase the genome-wide homozygosity and inbreeding
465 coefficient (Barragan et al., 2024). The strong genetic structure even with low genetic
466 differences can be attributed to the high homozygosity of the inbred lines formed

467 through selfing (Bomblies et al., 2010). The presence of multiple genetic groups in a
468 single location is mainly due to the presence of such inbred lines. This is supported
469 by studies like Bhattacharya et al., 2022. Selfing acts as a barrier to gene flow
470 between these inbred lines, thereby maintaining their genetic identity. However, the
471 genetic distance between these lines suggests that they are not genetically very
472 different. The presence of admixed individuals in many populations indicates the
473 occurrence of cross-fertilization as well. These crossing events can help in
474 generating new recombinant inbred lines. Future research including field-based
475 studies on mating systems in Lantana can help better understand the extent and
476 frequency of these various mating strategies.
477
478 4.3 Association of flower colour with genetic structure
479 Our study revealed an association between genetic clustering and flower colour
480 variation. Different flower colour variants were assigned to distinct genetic clusters
481 despite being from the same geographic location. This indicates the lack of gene flow
482 between flower colour variants which grow physically close to each other in many
483 locations. This correlation between flower colour and genetic structuring underscores
484 the influence of the mating system. Here, self-fertilization acts as a barrier to gene
485 flow and different inbred lines are associated with different flower colours. Thus, we
486 think that the identity of these lines is maintained by self-fertilization. Historically,
487 Lantana species were primarily defined mainly based on the flower colours and many
488 such variants were considered as different species (Sanders, 2006). Our study
489 suggests that these are within species variation and the overall phenotypic similarity
490 within a flower colour variant is maintained by self-fertilization. We think that the
491 correlation between flower colour and genetic structure is caused by the formation of

inbred lines. Further genetic analysis is required to understand the genetic basis of these flower colour variations.

4.4 Is Lantana a species complex?

The findings from the molecular analysis of Lantana challenge the notion of invasive Lantana being a species complex. While genetic structuring was evident, it predominantly arose from the prevalence of highly homozygous inbred lines rather than from the presence of genetically different species. Most lines exhibited low genetic distance between each other, indicating the high genetic similarity between flower colour variants. The high phenotypic variation observed could be the result of the introduction of multiple inbred lines to the subcontinent or the emergence of novel inbred lines through hybridization post-introduction. These variations could be within species phenotypic variations typical to many plant species. Through citizen science platforms like iNaturalist, it is evident that Lantana in its native range also exhibits similar flower colour variation. However, genomic analysis of related species of Lantana can help in understanding the chances of any past introgressions.

5 **Conclusions**

Studying genetic diversity patterns in invasive species is crucial for understanding their evolution. We explored genetic diversity patterns of the global invasive species *L. camara*. Our results reveal that lantana populations in India are strongly structured with genetic differences between flower colour variants. The low genetic distance observed between most plants negates the chances of lantana being a species complex. The presence of strong genetic structure even in the absence of high genetic distance is attributed to self-fertilization and the formation of putative inbred

lines. This is supported by the low heterozygosity and high inbreeding coefficient. In predominantly self-fertilizing species, individuals exist as inbred lines, which restricts gene flow and allows these inbred lines to maintain their genetic identity. We suggest that the correlation between flower colour and genetic structure is due to the association of specific flower colours to specific inbred lines.

Uniquely, our study highlights the significance of the mating system in shaping the genetic diversity pattern in invasive plant species. Our results also highlight the importance of multiple introductions and the introduction of genetically different variants in contributing to high genetic structuring within invasive populations. Further research on other invasive species will reveal how general these patterns might be.

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7 Author contributions

Conceptualization: P.P., U. R, and R. G., Data collection: P.P., Laboratory work: P. P., Data analysis: P.P, Project administration: P.P., U.R., and R. G., Funding acquisition: U. R, and R. G., Writing original draft: P.P., Writing – Review and editing: U.R., Supervision: U.R.

8 Data availability statement

Accession numbers for the raw ddRAD sequencing data and the GitHub link for analysis codes will be provided upon acceptance of the manuscript.

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