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Abstract

In studies of biological invasions, genomic data reveal introduction events, population structure and spatial expansion pathways, providing key insights to inform targeted and effective invasive species management. Fine-scale genetic studies elucidating the invasion processes remain scarce. This study investigates the local invasion dynamics of the avian-dispersed shrub *Pyracantha angustifolia* in a mountain basin of the Chaco Serrano, Córdoba, Argentina, integrating spatial distribution surveys with high-throughput RAD-sequencing genomic data. Sampling across an elevation gradient along a stream revealed species density decline with increasing elevation and distance from water, indicating recruitment hotspots near streams. Genetic analyses uncovered two distinct clusters with a patchy distribution, moderate differentiation and differing genetic diversity, suggesting at least two, genetically diverse, independent introductions. Kinship analyses revealed pervasive familial relationships within clusters but none between them, indicating fine-scale kin structure driven by localized dispersal and lack of post-introduction interbreeding between groups. Partial Mantel tests indicated a weak isolation-by-distance pattern at the landscape scale, while dispersal kernel modeling supported predominance of short-distance dispersal and occasional longer dispersal events. The findings provide practical data to improve ongoing management and control strategies to preserve the invaded ecosystem.

Keywords

Pyracantha angustifolia, kinship analysis, dispersal kernel, mountain riparian habitats, invasive species management

Resumen

En los estudios sobre invasiones biológicas, los datos genómicos pueden revelar eventos de introducción, estructura poblacional y vías de expansión espacial, brindando información clave para la gestión de especies invasoras. Sin embargo, los estudios genéticos a pequeña escala para comprender estos procesos son escasos. En este trabajo se analiza la dinámica de invasión local de *Pyracantha angustifolia*, un arbusto principalmente dispersado por aves, en una cuenca montañosa del Chaco Serrano (Córdoba, Argentina), integrando análisis de distribución espacial y datos genómicos obtenidos mediante RAD-sequencing. El muestreo en un gradiente altitudinal mostró una disminución en la densidad de la especie con el aumento de la altitud y la distancia del agua, identificando puntos críticos de reclutamiento cerca del arroyo. Los análisis genéticos revelaron la existencia de dos grupos genéticos, con distribución irregular, diferenciación moderada y diferentes niveles de diversidad genética, lo que sugiere la ocurrencia de al menos dos introducciones independientes y genéticamente diversas. Los patrones de parentesco y dispersión indican estructura familiar a escala pequeña, impulsada por dispersión localizada y sin evidencia de cruza post-introducción entre los grupos, lo que apoya la hipótesis de varias introducciones genéticamente diversas. Pruebas de Mantel parcial indicaron un patrón débil de aislamiento por distancia a escala del paisaje, mientras que el modelado de kernels de dispersión respaldó el predominio de dispersión a corta distancia y eventos ocasionales de dispersión a mayores distancias. Los resultados proporcionan datos prácticos para mejorar las estrategias de control en curso para preservar el ecosistema invadido.

Introduction

Biological invasions are among the main threats to biodiversity and ecosystem functioning at the global scale (IPBES 2019; Pyšek et al. 2020; Jaureguiberry et al. 2022). The introduction and spread of invasive non-native species can deeply alter native communities, disrupt key ecological processes, and compromise ecosystem stability (Simberloff et al. 2013; Vilà et al. 2024; Carneiro et al. 2025). Mountains are usually considered resistant to biological invasions, mostly due to their extreme climate and low accessibility, but the recent anthropogenic footprint, including climate change, land-use changes and infrastructure/urban development, has made these otherwise relatively well-preserved ecosystems more vulnerable to invasions (Pollnac et al. 2012; Petitpierre et al. 2016). Understanding the dynamics and the history of an invasion process is crucial for the development of effective management strategies (Heger et al. 2021), since this knowledge helps to predict the spread of the invasion and identify vulnerable areas to invasion.

Genetic analyses provide powerful information to understand invasion dynamics by revealing demographic history, introduction routes, and dispersal patterns of non-native invasive species (Cristescu 2016; North et al. 2021; Hodgins et al. 2025). Specifically, genomic data enable identification of propagule sources, differentiation between single versus multiple introduction events, and tracing of spatial expansion pathways, which is crucial information for targeted and efficient control efforts (Cristescu 2016). Many studies across various non-native invasive taxa, using diverse molecular tools, have explored these aspects at different spatial scales, providing valuable insights for management (e.g., Atsawawaranunt et al. 2023; Kendrick et al. 2024; Mairal et al. 2023; McCulloch et al. 2023). However, case studies focusing on small, localized areas are rare (e.g., Tsykun et al. 2019). Recent perspectives on invasion studies emphasize moving beyond species-level assessments to focus on population-level analyses, as these provide deeper insights into invasion dynamics (Haubrock et al. 2024). This approach could help fill gaps in local invasion management by enabling the design of practical, local control actions.

In Córdoba Province (Argentina), a large number of non-native invasive plant species have been registered, many of which have successfully established and spread across extensive areas, particularly in the mountainous systems (Giorgis et al. 2011; Cingolani et al. 2022). Knowledge of their invasive processes and designing control strategies is fundamental since the hydrological network of the mountains of Córdoba provide water to most of the provincial population (Llanes et al. 2022). The diversity of invasive non-native species in Córdoba includes herbs, shrubs as well as trees, found in all types of environments (Giorgis and Tecco 2014). One such species is the Asian shrub *Pyracantha angustifolia* (Rosaceae), a well-known invasive species in several regions of the world (Chari et al. 2020), which has invaded Chaco Serrano landscapes in the province (Giorgis and Tecco 2014; pers. obs.). *Pyracantha* species are cultivated in Argentina mainly for ornamental purposes, and *P. angustifolia* in particular was recorded as naturalized already around 1990 (Jocou and Gandullo 2019). *Pyracantha angustifolia* is currently included in the Argentinean official list of non-native invasive species (<https://www.argentina.gob.ar/ambiente/biodiversidad/exoticas-invasoras/lista>; accessed 1 November 2025). This species, as well as others non-native invaders (e.g., *Ligustrum lucidum* and *Cotoneaster franchetii*), present vegetative resistance and fruits/seeds that are dispersed by native birds in autumn-winter, when fruits

of most native species are not available, which would promote the dispersal effectiveness of these invaders (Gurvich et al. 2005; Vergara-Tabares et al. 2016). *Pyracantha angustifolia* (like other *Pyracantha* species) is characterized by abundant flowering and fruiting (Jocou and Gandullo 2019; pers. obs.), is self-compatible and exhibits high percentages of fruit set by self-pollination (75-95%; pers. obs.), a combination of features that render each individual a potentially efficient seed producer. Thrushes of the genus *Turdus* (Turdidae) are the main dispersers of large quantities of *P. angustifolia* seeds in the mountains of Córdoba (Vergara-Tabares et al. 2016, 2018), although a wide variety of birds and even some mammals also consume its fruits and represent secondary dispersers (De Luca et al. 2025). Two findings are relevant to try to understand the invasion of the species: thrush feces density decreases drastically with distance from the nearest *P. angustifolia* fruiting individual (Vergara-Tabares 2017), and seeds maintain a high germination rate after passing through the digestive tract of thrushes (ca. 90%; Vergara-Tabares 2017). By combining all the evidence, it can be inferred that the advance of the invasion of *P. angustifolia* would be related to a high pressure of locally generated propagules (i.e., seeds), facilitated by the association established with native dispersers, mainly thrushes. Considering these data, along with the fact that the species does not form seed banks (Giantomasi et al. 2008), it could be expected a spatial pattern of individual relationships and genetic structure of the invasive *P. angustifolia* determined by the distance of seed dispersal.

In this study, we investigate the invasion dynamics of *P. angustifolia* in a mountain basin within the Chaco Serrano, in the Sierras Grandes of Córdoba, integrating spatial distribution surveys with high-throughput sequencing genomic data (i.e., RAD-sequencing). Our main objective was to explore the fine-scale spatial and genetic dynamics of the invasive *P. angustifolia*, focusing on identifying potential introduction events and dispersal patterns in the studied area. Particularly, we aimed to: 1. describe the spatial distribution by age group of *P. angustifolia* within the studied basin, 2. characterize the genetic structure and genetic diversity at a local scale, 3. assess evidence for introduction events, and 4. examine spatial patterns of relatedness and dispersal within the basin. We hypothesize that the invasion of *P. angustifolia* is characterized by a spatially explicit genetic structure corresponding to its reproductive system and the movement of propagules (i.e., predominance of short distance dispersal) and the occurrence of fine-scale kinship patterns indicative of recent localized dispersal (i.e., the closer a pair of individuals are in the field, the more likely they are close relatives, and vice versa). Our study will integrate fine-scale spatial surveying with genome-wide RADseq data to elucidate the invasion dynamics of *P. angustifolia* in a region and species where population genetic information is currently limited, thus addressing an important knowledge gap. The findings will ultimately be integrated into management projects we are conducting in the region.

Materials and Methods

Study area

The study was conducted in the Los Hornillos basin (31°54'04.9"S 64°58'29.5"W; Fig. 1A), located on the western flank of the Sierras Grandes in the San Javier Department, Córdoba Province, Argentina. In this

region, *P. angustifolia* has extensively colonized the margins of the watercourses and, to a lesser extent, the adjacent mountain slopes (Fig. 1B). Field observations and sampling were carried out along the main watercourse over an elevation range of 1,100 to 1,650 meters above sea level (masl), covering ca. 4 km of its meandering extension (Fig. 1A). In the upper limit of the sampling area *P. angustifolia* is virtually absent. The study area is located within a protected area, the Los Hornillos Reserve, which borders another protected area at its upper end, the Pampa de Achala Provincial Reserve. At the lower end of the sampling area lies the town of Los Hornillos (ca. 1,900 inhabitants in 2022; <https://censo.gob.ar/index.php/gobiernos-locales/>; accessed 1 November 2025), which obtains its drinking water from the stream running through the basin. The native vegetation up to about 1,500 masl is characterized as Mountain Chaco Woodland, dominated by woody species such as *Lithraea molleoides*, *Vachellia caven*, *Celtis tala*, *Ruprechtia apetala*, *Zanthoxylum coco*, and *Bougainvillea stipitata* (Cabido et al. 2018). Above this elevation, the landscape transitions to high-elevation shrublands, characterized by the presence of *Baccharis aliena*, *Berberis* spp., *Flourensia oolepis*, and small stands of *Polylepis australis* in the ravines where streams originate at approximately 1,700 masl (Cabido et al. 2018). The topography of the area is heterogeneous, with steep slopes and V-shaped valleys, as commonly found along the watercourses of the western Sierras Grandes (Gaido et al. 2006). The climate is markedly seasonal, with dry and cold winters, frequent frosts, and occasional snowfall. Average annual rainfall is approximately 700 mm, concentrated in spring and summer, while the mean annual temperature is 18.5°C (Cortes 2018).

Spatial distribution of *P. angustifolia*

We first characterized the distribution pattern of the target species along the elevation gradient of the stream. To do this, we established T-shaped transects every 25-50 meters of elevation (this was variable as the slopes are steeper at higher elevations) from 1,150 to 1,600 masl, placed successively on alternate sides of the watercourse (Fig. 1C). Each transect consisted of three sections of 2 x 10 m each one (Fig. 1C, D): one parallel to the watercourse (S1) and two perpendicular to it, aligned in sequence (S2 and S3). This approach was adapted from a methodology for sampling along mountain trails (Liedtke et al. 2020). In all three sections, the number of individuals of *P. angustifolia* and their estimated age (i.e. renewals < 20 cm, non-fruiting juveniles, fruiting adults) were recorded. A total of 14 transects (T1-T14) were done.

To characterize the species abundance and distribution pattern we calculated density and frequency. Density and frequency indirectly also denote presence/absence. Both metrics were discriminated by age group. We calculated density as individuals per m², counting all individuals observed, computing separately each transect and each sector of the transects. The frequency indicates the probability of finding the species in any given sampling unit (i.e., transects and sectors), providing a measure of spatial occupancy, and we calculated it as the percentage of sampling units in which *P. angustifolia* was present:

$$Frequency (\%) = \left(\frac{\text{Number of sampling units where the species is present}}{\text{Total number of sampling units surveyed}} \right) \times 100$$

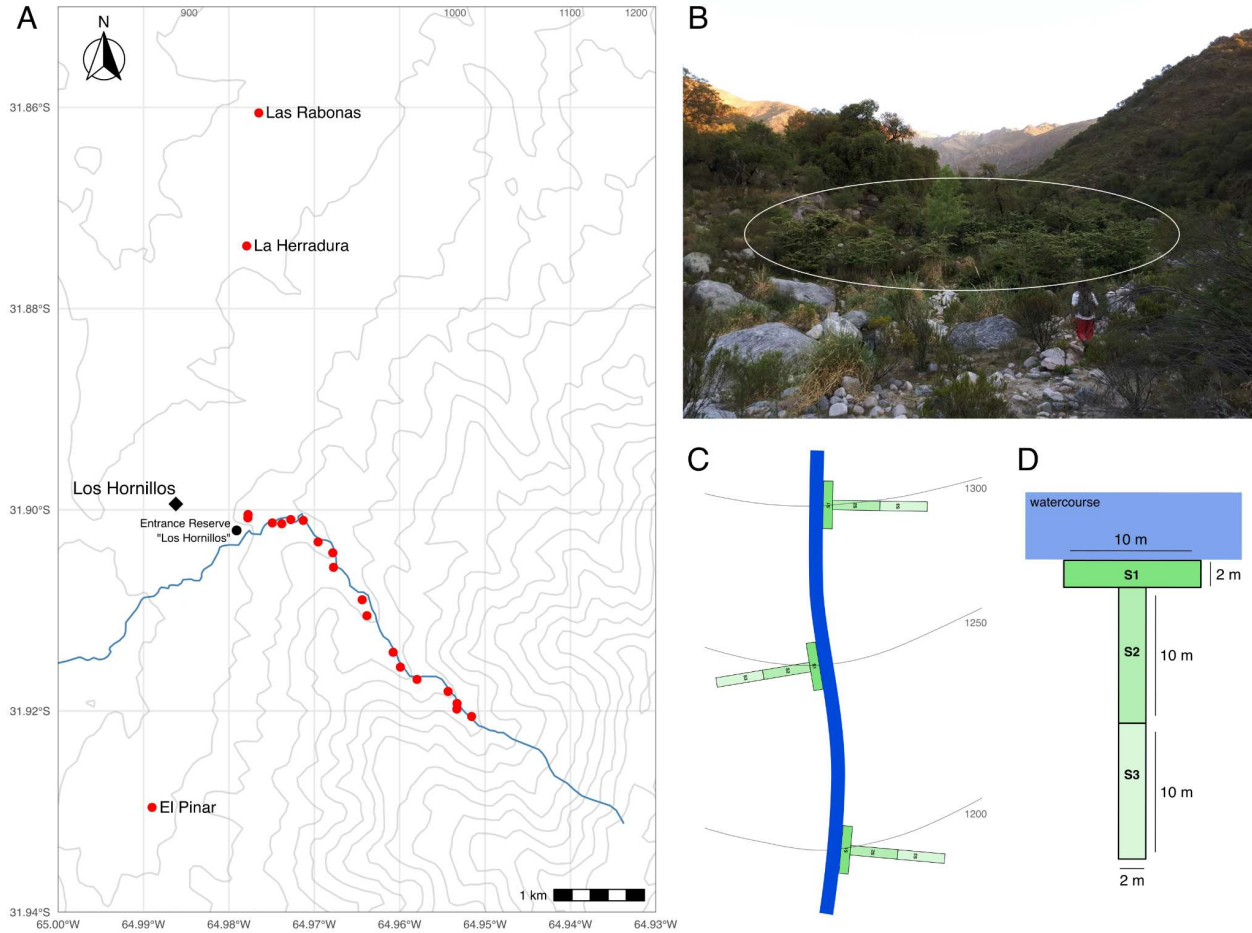


Fig. 1 Study site and design of the characterisation of the local distribution of invasive *Pyracantha angustifolia*. **A:** Location of the study area centered in the Los Hornillos basin; the nearby locality Los Hornillos (black diamond) and collection sites for genetic sampling (red circles) are indicated. Level curves are shown every 100 m of elevation (reference values are in the upper margin). The main watercourse of the basin is drawn in blue. **B:** typical stand of *P. angustifolia* (encircled) by the watercourse and one of us approaching. **C, D:** scheme of T-shaped transects used to study the distribution of *P. angustifolia* along the main watercourse of the Los Hornillos basin, showing the general arrangement in C (hypothetical level curves drawn), and the detail of a single transect with the three sections (S1, S2, S3) distinguished in D. The main watercourse is drawn in blue

Genetic data acquisition and processing

Genetic sampling, sample preparation and DNA sequencing

Based on the spatial distribution data, we selected representative sites along the main watercourse of the basin for genetic analysis, despite the differences in density along the elevation range, to ensure broad spatial representation. In total, we established 17 collection sites (Fig. 1A). In addition, we included as external references three sites outside the basin, also invaded with *P. angustifolia*, namely: Las Rabonas, La Herradura and El Pinar (Fig. 1A). These sites are respectively 4.5, 3, 3.4 km from the lower end of the sampling area in the basin, between 900 and 1,100 masl. We collected leaf samples from fruiting adult individuals at each site (from 1 to 8 individuals, depending on the number of plants found); leaves were dried and stored with silica gel. The high density of plants could potentially introduce a bias and lead to the

sampling of closely related individuals, which may be a confounding factor. We expect kinship relationships across our sampling, therefore this aspect is specifically explored and accounted for as part of our comprehensive examinations. We consider this fundamental to better understand the invasion dynamics, especially for the intended fine-scale study.

We collected a total of 62 samples, 55 from Los Hornillos and seven from the external sites. Genomic DNA was extracted from silica-dried leaf tissue using the InviSorb® Spin Plant Mini Kit, following the manufacturer's instructions. Extracts were cleaned using the Macherey-Nagel® NucleoSpin gDNA clean-Up kit, and DNA quality and concentration were subsequently assessed with a Qubit fluorometer. We prepared single-digest RADseq libraries following the protocol by Paun et al. (2016), with modifications in the shearing step (i.e., six cycles 90 s off, 60 s on). The libraries were sequenced on an Illumina platform HiSeq 100bp System (Vienna Biocenter Core Facilities, Austria), generating 100 bp single-end reads.

In the study area, *P. angustifolia* cohabits with its congener *P. crenulata*, although the latter is scarce. These species complete their flowering (which lasts about three weeks) in succession, with a brief overlapping period between them at the end of *P. angustifolia* flowering (pers. obs.). Given that interspecific hybridization is possible in *Pyracantha* (Chari et al. 2020), to rule out the possibility of having sampled hybrid individuals, we collected and processed simultaneously four samples of *P. crenulata*, to be analyzed together with *P. angustifolia*. We did genetic structure and NeighbourNet analyses (Suppl. Information), and in all cases the samples of *P. angustifolia* form a distinct and distant group from those of *P. crenulata* (Figs. S1, S2). We therefore confidently rule out the existence of hybrids and ensure that the samples used in this study belong to *P. angustifolia*.

Demultiplexing and SNP calling

We demultiplexed raw RADseq reads based on unique barcodes using the module `process_radtags` from Stacks v.2.60 (Catchen et al. 2013). Barcodes and adapters were removed during this step, and low-quality reads (Phred < 30) were discarded. We processed demultiplexed reads using `ipyrad` v.0.9.85 (Eaton and Overcast 2020) to perform *de novo* assembly and SNP calling using default settings for most parameters. To generate a relaxed dataset suitable for downstream filtering, we set the minimum number of individuals with data per locus to two (parameter `min_samples_locus`). The resulting variant call format (VCF) file was used for downstream filtering.

Using VCFtools v.0.1.16 (Danecek et al. 2011), we filtered biallelic SNPs with a minor allele frequency (maf) ≥ 0.02 (threshold selected based on the observed allele frequency distribution examined beforehand; not shown) and present in at least 70% of individuals (i.e., allowing up to 30% missing data). To minimize linkage among SNPs, we further filtered the datasets to retain only one SNP per RAD locus (the first one, to ensure replicability) using RADtools (Baxter et al. 2011). We explored different values for maf and missing data thresholds, and since the results were consistent across settings, we selected this filtering scheme as it offers a balanced trade-off between stringency and data completeness.

Population structure and genetic diversity analyses

We used the package LEA v.3.18.0 (Frichot and Francois 2015) in R v.4.0.3 (R Core Team 2024) to investigate population structure. This package can handle the presence of family members in the study group. The `snmf` function was run to estimate individual ancestry coefficients for values of K ranging from 1 to 6, for a total of 100 repetitions and 100 iterations. The optimal number of genetic clusters was determined using the cross-entropy criterion, selecting the K value with the lowest score as the best fit. Individual admixture proportions were visualized in a barplot. To explore the spatial distribution of genetic structure, the individual admixture proportions inferred were also visualized geographically using the R package MapMixture v.1.2.0 (Jenkins 2024).

We excluded performing Principal Component Analysis because when family members are included, the main principal components often reflect close relatives instead of actual population structure (Astle and Balding 2009; Conomos et al. 2016; Abegaz et al. 2019). We explored the applicability of PC-AiR using the package GENESIS v.2.38.0 (Gogarten et al. 2019), which uses measures of pairwise ancestry divergence as well as kinship coefficients to identify an ancestry representative subset of mutually unrelated individuals. By default, the threshold to define unrelated individuals (parameter `kin.tresh`), is equivalent to approximately fourth-degree relatives, thus excluding all the samples used in our study (see Kinship and relatedness analyses subsection). We then tested different values for this parameter but it was evident that any value used would be an arbitrary threshold, and therefore we decided to exclude this approach as well.

Using the R package hierfstat v.0.5-11 (Goudet 2005), we calculated observed and expected heterozygosity (H_o and H_e) to assess genetic variation levels and potential deviations from Hardy-Weinberg equilibrium, the inbreeding coefficient (F_{IS}) to quantify deviation from random mating within genetic groups, and allelic richness to quantify the number of distinct alleles present within each genetic group. We counted private alleles to identify unique genetic variants specific to each genetic group using the package poppr v.2.9.8 (Kamvar et al. 2015). To evaluate genetic differentiation and gene flow among groups, we estimated the proportion of shared alleles between groups with PopGenReport v.3.1.3 (Adamack and Gruber 2014) and pairwise group differentiation (F_{ST}) using hierfstat.

Kinship and relatedness analyses

We calculated pairwise kinship coefficients with the program KING v.2.3.2 (Manichaikul et al. 2010) testing all possible pairs of individuals. Files of types `bed`, `bim` and `fam` were written from the VCF file using PLINK v.1.9 (Purcell et al. 2007). Pairwise kinship coefficients were then computed using the `--kinship` function. This approach enables the detection of close familial relationships up to the third degree, namely: first-degree relatives (e.g., parent–offspring, full siblings) with kinship coefficients > 0.177 ; second-degree (e.g., half-siblings, grandparent–grandchild) with values between 0.0884 and 0.177; and third-degree relatives (e.g., first cousins) with coefficients ranging from 0.0442 to 0.0884. As specified in the program instructions (<https://www.kingrelatedness.com/manual.shtml#WITHIN>; accessed 1 November 2025), inferring more distant relationships is challenging, therefore we have not calculated them. The resulting kinship matrix was visualized as a heatmap using the R package pheatmap v.1.0.13 (Kolde 2025) to identify clusters of closely related individuals, after converting the output `kin` file to a square matrix with the R

package tidyverse v.2.0.0 (Wickham et al. 2019).

We generated a network graph to visualize spatial relatedness between individuals and potential dispersal in Gephi v.0.10.1 (Bastian et al. 2009), using pairwise kinship coefficients and spatial coordinates. We generated an edge list, where the nodes were the individuals and the strength of the connection between nodes (pairs of individuals) was defined by the kinship coefficient retrieved. Spatial coordinates of each individual (i.e. collection site) were used to position the nodes in a map. We then imported both the edge list and the node attribute table (including individual identities and spatial coordinates) into Gephi. Edges were weighted by the degree of kinship. We obtained maps showing the spatial arrangement of direct kinship connections among all individuals.

Isolation by Distance Analysis

We performed a partial Mantel test to evaluate isolation by distance (IBD), comparing the matrices of pairwise genetic distances and spatial distances, using the kinship coefficients as a covariate. In this way, we intend to assess the correlation between the first two distance matrices controlling the effect of kinship relatedness, therefore evaluating whether the association between genetic and spatial distances remains after removing the influence of kinship. The coordinates of the sites were used to calculate spatial distances, and genetic distances were computed using adegenet v.2.1.11 (Jombart 2008). The partial Mantel test was implemented using the R package vegan v.2.6.10 (Oksanen et al. 2025) with 9,999 permutations, applying the Pearson correlation coefficient. The function mantel.partial used does not handle missing values and therefore these must be either removed or imputed. Since kinship relationships were not recovered for all pairs of samples (see Results section), we imputed missing values in the kinship matrix by replacing NAs with zero (representing the assumption of no kinship), allowing us to retain all samples in the analysis. We performed equivalent tests for subsets of samples assigned to the recovered genetic groups.

To evaluate how genetic relatedness varies as a function of spatial separation between pairs of individuals within the basin, we plotted kinship coefficients against geographic distances for all pairs of individuals sampled from within the basin, excluding those from the three external sites. The plot was generated using ggplot2 v.4.0.0 (Wickham 2016). Smoothed LOESS curves were fitted separately for each kinship degree within each genetic group, enabling visualization of kinship trends across geographic distances.

Dispersal kernel estimation

We analyzed kinship data and geographic coordinates to estimate dispersal kernels both for all samples and separately for the subset from the basin. We calculated geographic distances between kin pairs with the geosphere package (Hijmans 2024) using the Haversine formula. To include samples with zero geographic distance (i.e., collected in the same site), we added a small random jitter (1–5 m). Following the approach of Filipović et al. (2020), which defines the corresponding number of possible dispersal events for each kinship category as the number of breeding sites plus one, we adjusted the identities in our range (see Kinship and relatedness analyses subsection) to assign the categories. Dispersal distances were scaled and used to fit

exponential, log-normal, and gamma kernels with maximum likelihood estimation implemented in the package *fitdistrplus* v.1.2.4 (Delignette-Muller and Dutang 2015). Each kernel highlights a different feature of the dispersal distance distribution: rate of decay (exponential), tail heaviness (log-normal), and shape flexibility (gamma). We applied the Freedman-Diaconis rule to determine an optimal number of bins for the histogram, representing the probability density distribution of scaled geographic distances between pairs of individuals, yielding 17 bins for the full sample set and eight bins for the basin subset. We calculated Akaike Information Criterion (AIC) values for each dispersal kernel fitted to the histograms to determine the best-fitting kernel. The histograms and the fitted kernels were visualized as probability density functions of scaled distances using *ggplot2*.

Results

Spatial distribution of *P. angustifolia*

Pyracantha angustifolia was found in 12 of 14 transects, between 1,150 and 1,530 masl, absent only at the highest elevations (T13 and T14; Fig. 2A). However, isolated individuals also occurred up to 1,650 masl, which did not fall within any transect; these individuals were nonetheless sampled for genetic analysis. Breaking down by age group, juveniles appeared in every transect where the species occurred, regardless of the sector, adults were missing from some higher-elevation transects, while renovals were confined to lower elevations, except for a single site at 1,500 masl (T12, characterized by a flooded and muddy soil) (Fig. 2A). The species overall frequency was 85.71%, decreasing by sector (i.e. with increasing distance from the watercourse): 85.71% in S1, that is in all 12 transects where the species was found, 64.26% in S2, and 14.29% in S3 (Fig. 2B). S1 showed the highest frequencies for all age groups, while frequencies were lower in S2, very low for renovals (Fig. 2B). In S3, renovals were absent while juveniles and adults were found at their lowest frequencies (Fig. 2B).

The density of *Pyracantha angustifolia* varied with elevation, distance from the watercourse (i.e., among sectors within transects), and age group. There is a clear general decline in density from lower (T1) to higher elevations (T14), and also with increasing distance from the watercourse within the same transect, especially visible in the total density and for the renovals (Fig. 2A, C). When considering all individuals regardless of age, density generally decreased with increasing elevation and distance from the watercourse, approaching zero at higher elevations and farther sectors (Fig. 2A, C). Overall, the highest total density of the species was consistently found in S1, with peaks in S1 at lower elevations (Fig. 2A, C). Density in S2 and S3 is generally lower across all transects, with many transects showing near zero values (Fig. 2A). The decrease in density and eventual absence of the species at higher elevations would indicate the uppermost invasion front within the basin.

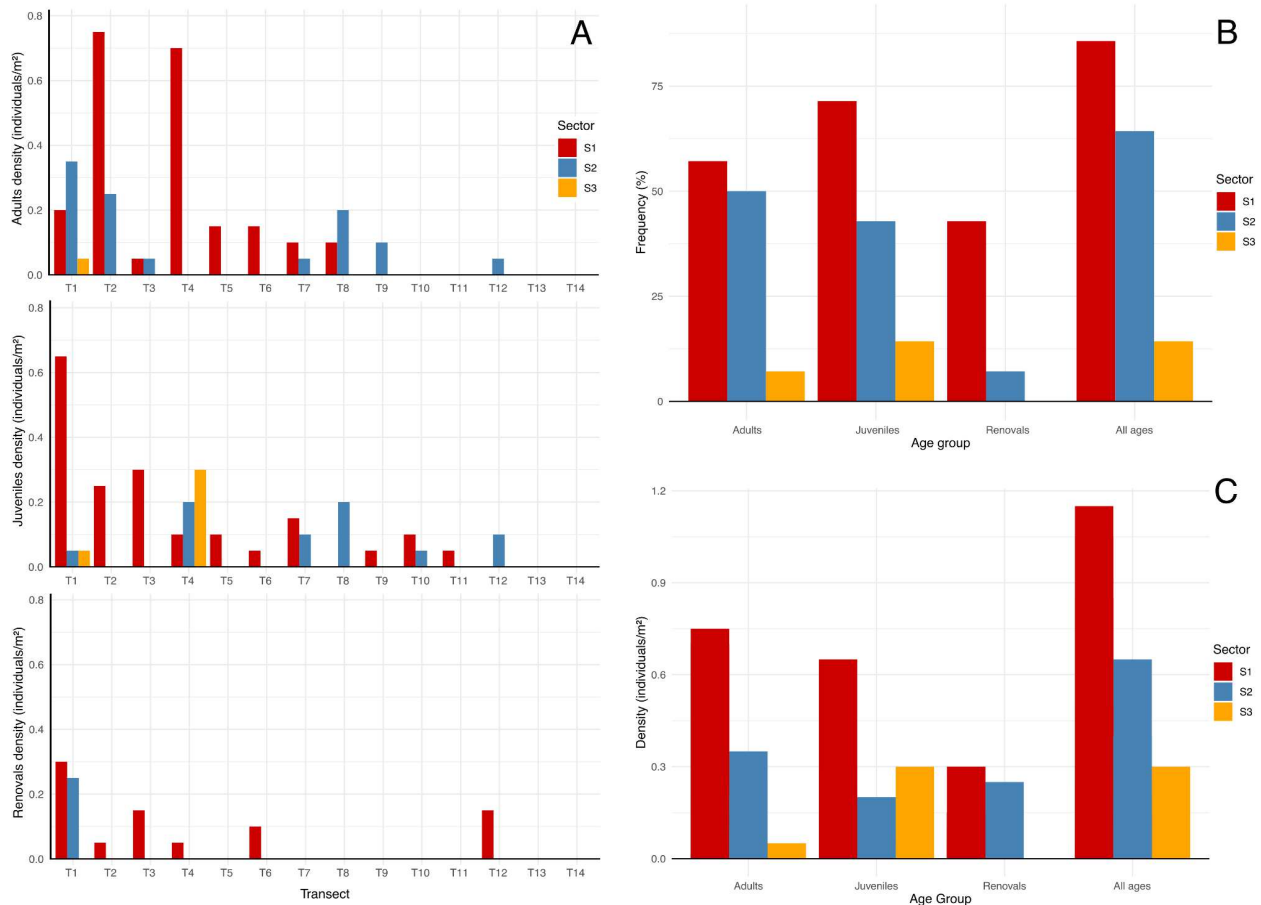


Fig. 2 Frequency and density of invasive *Pyracantha angustifolia* along the main watercourse of the Los Hornillos basin. Metrics are shown for all individuals combined (B, C) as well as disaggregated by age group (A–C), and by sector (S1–S3, increasing distance from the watercourse). **A:** Density (individuals/m²) of adults, juveniles, and renovals along the elevation gradient (transects T1–T14, from lowest to highest elevation), also indicating presence/absence of the species. **B:** Frequency (%). **C:** Overall density (individuals/m²)

Population structure and genetic diversity analyses

The best-fitting value of ancestral populations for the LEA analysis was $K = 2$. Ancestry estimates revealed a clear genetic structure across the sampled individuals, with a sharp transition in ancestry proportions between the two clusters retrieved, identified as G1 and G2 (Fig. 3A). The spatial interpolation of ancestry coefficients using MapMixture revealed that all collection sites were dominated by a single genetic cluster, both within the basin and at the external sites (Figs. 3B, C). Individuals from the uppermost section of the sampled area within the basin, several intermediate sites, and the sites located outside the basin were assigned to G1. In contrast, individuals assigned to G2 were found at alternating locations along the basin, including the densest sites at lower elevations. Geographically adjacent sites did not always share the same genetic group assignment.

The two genetic groups exhibit different levels of genetic diversity, with H_e and H_o values higher in G1; H_o was higher than H_e in both genetic groups (Table 1). Allelic richness and the number of private alleles were also higher in G1 in contrast to G2 (Table 1). Both groups showed negative inbreeding coefficients (F_{is}), which is consistent with the H_o being higher than H_e (Table 1). The proportion of shared

alleles between both genetic groups is 0.7714 (77.14%), indicating substantial allele sharing overall. The pairwise F_{st} between the two genetic groups was 0.2012, suggesting moderate to substantial genetic differentiation and limited gene flow between them.

Table 1 Summary of genetic diversity and population structure metrics for each genetic group of invasive *Pyracantha angustifolia* in the Los Hornillos basin and neighboring sites. Ho: observed heterozygosity; He: expected heterozygosity; F_{is} : inbreeding coefficient

Genetic group	He	Ho	Allele richness	Private alleles	F_{is}
G1	0.1974	0.2580	1.9585	949	-0.1583
G2	0.0543	0.0681	1.3712	56	-0.1079

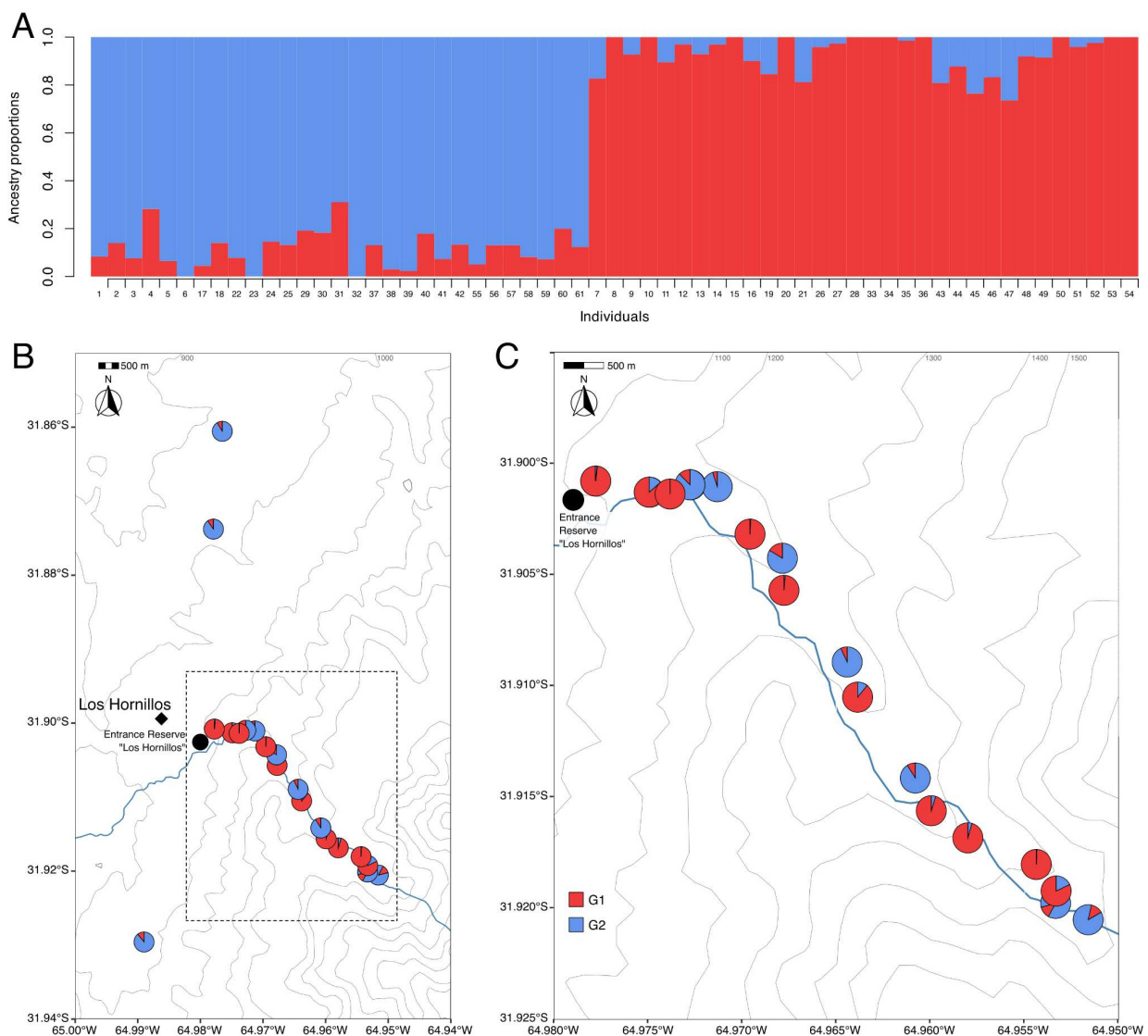


Fig. 3 Genetic structure of invasive *Pyracantha angustifolia* in the Los Hornillos basin and neighboring sites. **A:** bar plot of ancestry proportions for $K = 2$. **B, C:** pie charts representing ancestry proportions for each collection site plotted on maps, including the external sites (B) and a close-up of the targeted basin (C), which corresponds to the dotted area in B. Two genetic groups are identified (G1 and G2), with corresponding colours to A. The nearby locality Los Hornillos (black diamond) is indicated. Level curves are shown every 100 m of elevation (reference values are in the upper margin)

Kinship and relatedness analyses

The kinship coefficients obtained show first- to third-degree familial relationships limited to pairs of individuals assigned to the same genetic group (G1 or G2). This means that no kinship relationships were found between individuals from different groups (at least up to the degree calculated). In correspondence, the heatmap of kinship coefficients revealed two well-differentiated genetic clusters, corresponding to groups of individuals with higher relatedness within clusters and no relatedness between them (Fig. 4A). One group corresponds to G1, within which pairwise kinship relationships were recovered for all possible pairs of individuals, with a strong predominance of first-degree relationships (93%), and the remaining being second-degree (Fig. 4A, B). The second cluster, which corresponds to G2, exhibited a more heterogeneous pattern (Fig. 4A): not all possible pairwise kinship relationships were recovered, and two individuals showed no detectable kinship with others (even though they do not show substantial differentiation in the genetic structure analysis). Within this group, first-degree relationships accounted for ca. 47% of the total, followed by ca. 37% second-degree and nearly 15% third-degree relationships (Fig. 4B).

Network graphs were drawn in Gephi separately for G1 and G2 since no kinship relationships were recovered between them (Fig. S3). In both cases, all the nodes, representing collection sites and their respective individuals, show a convergence of first- and second-degree relationships, and eventually also third-degree for G2. This means that every site (i.e., some or all of the individuals in each one) is genetically linked to others by those degrees of relationship. The patterns of both networks reveal widespread interconnectedness, indicating that kin relationships are pervasive throughout the sampled area, within each genetic group recovered.

Isolation by distance analysis

The partial Mantel test of the entire sample set revealed a low but significant correlation between genetic and spatial distances after controlling for kinship, with a statistic of $r = 0.254$ ($p = 0.001$). This indicates that spatial distance contributes to genetic differentiation independently of kinship, suggesting a moderate pattern of IBD at the landscape scale. Conversely, when both genetic groups were analyzed separately, partial Mantel correlations were close to zero and not statistically significant ($r = 0.0872$, $p = 0.246$ for G1; $r = -0.02178$, $p = 0.581$ for G2). This suggests no detectable IBD pattern within genetic groups after controlling for kinship.

The relationship between kinship coefficients and geographic distances outlined within the basin indicates that both genetic groups display kin pairs of individuals throughout the entire range of spatial distances (Fig. 4C), which is consistent with the lack of isolation by distance within each genetic group. Kinship coefficients, for all ranks and both genetic groups, remain largely stable across geographic distances, as shown by the relatively flat LOESS-smoothed curves (Fig. 4C).

Dispersal kernel estimation

The dispersion kernel trends are consistent between the complete sample set and the basin subset. In both cases, the slopes of the three kernels differ, but all peak near zero distance, indicating a high probability of

short-range dispersal, followed by a steady decline in probability with increasing distances (Figs. 4D, S4). The histograms show that most pairs of relatives occur at shorter distances, with frequencies decreasing at longer distances; this decline is sharper for the complete sample set (Figs. 4D, S4). Among the tested models, the gamma dispersal kernel provided the best fit (lowest AIC value) to the empirical distribution of scaled kin-pair distances depicted in both cases. Its flexible shape allowed it to better capture both the peak at short distances and the gradual decline at longer distances. These results support a dispersal pattern dominated by short-range movements with occasional longer dispersal events.

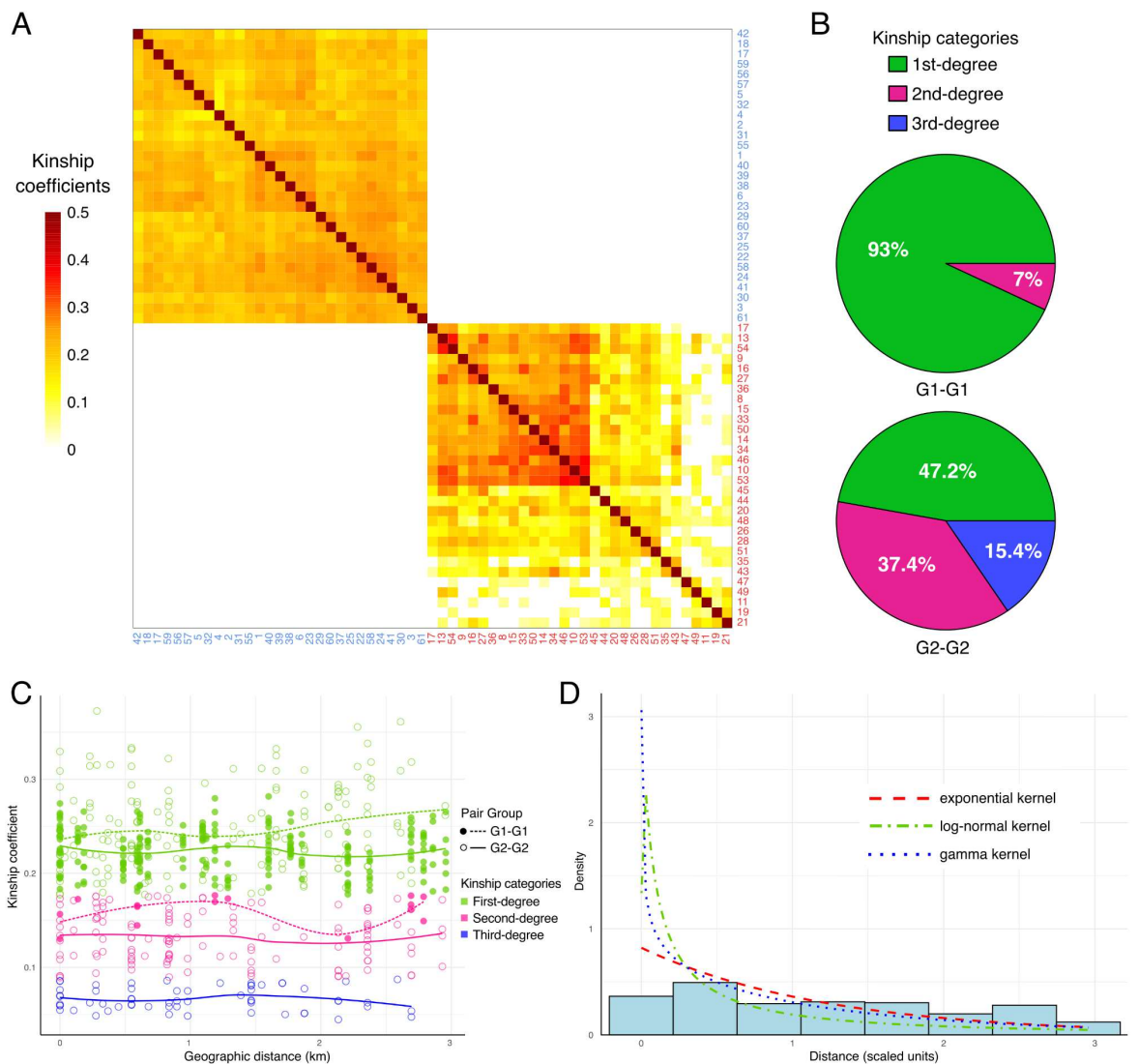


Fig. 4 Kinship and dispersal patterns of invasive *Pyracantha angustifolia* in the Los Hornillos basin and neighboring sites. **A**: heatmap of pairwise kinship coefficients, with the closest degree of correlation corresponding to the highest values. No recovered pairwise relationships are blank. Individuals labelled on the x and y axes, identified with colours corresponding to the genetic groups retrieved (G1 blue, G2 red). Note that no pairwise relationships were found between individuals from different genetic groups. **B**: pie charts showing the proportions of kinship degrees according to the pairwise coefficients calculated between individuals from each of the two genetic groups (G1-G1 and G2-G2). **C**: relationship between pairwise kinship coefficients and geographic distances (in kilometers). Point shapes indicate the genetic groups (G1 or G2) of the pairs of individuals, colored according to the kinship degree. Solid and dashed lines represent LOESS-smoothed curves fitted to each kinship degree for pairs of individuals in each genetic group. **D**: dispersal kernels (exponential, log-normal, and gamma) within the basin. The histogram represents the probability density distribution of scaled geographic distances between pairs of individuals (eight bins). Note that the box portion below zero is an artifact of the plot

Discussion

A major goal in understanding species invasion dynamics is to generate evidence for management and control strategies development. Our results depict an invasion process of *P. angustifolia* in the studied Chaco Serrano basin shaped by multiple introductions of genetically diverse propagules and predominantly localized dispersal that produces fine-scale kin-structured genetic patterns. Based on the observed distribution pattern, it appears that there may be facilitating factors that enable the establishment and expansion of the species along riparian habitats, particularly near water. We also highlight that long-distance dispersal events would contribute to broader range expansion. Integrating genetic (genome-wide) data with the environmental context has improved our understanding of the invasion process of *P. angustifolia* and provided useful information to tailor and optimize the management strategies we are currently developing on site to restore this sensitive mountain ecosystem.

The spatial survey showed that *P. angustifolia* predominates along watercourses at lower-to-mid elevations (1,150–1,530 masl), with density and frequency declining sharply both with elevation (namely, increasing distance from the urban area) and increasing distance from the watercourse. The higher densities near the watercourse may be associated with conditions favorable for seedling establishment. This was clearly illustrated by a transect at high elevation (T12) characterized by flooded and muddy soil, which deviates from the trend, showing increases in the densities of the three age groups. Scarcity of renewals at higher elevations points to (still) limited recruitment in what we identify as the upper invasion front, a temporary boundary that would move upwards as the invasion progresses. The results highlight the importance of distance to water in shaping the spatial distribution and recruitment of *P. angustifolia*. In fact, a management study conducted in the same basin (after our field work was completed) found that plants subjected to cutting and livestock browsing recovered faster as regards resprouting and renewed flowering and fruiting when they were near the stream (Fernández et al. 2024), emphasizing the fundamental role of water availability in facilitating the invasion of the species. The susceptibility of riparian zones to be invaded by non-native plant species has already been pointed out, because they provide a suitable environment for colonization as well as corridors that facilitate dispersal, among other reasons (Tickner et al. 2001). Given the importance of watercourses as recruitment hotspots for the invader, these sensitive habitats need particular attention. The affinity of *P. angustifolia* with water is not only important from an ecological point of view and for invasion management, but also because of the fundamental role of the basin as a source of drinking water for the local community.

Genetic analyses uncovered two well-differentiated groups, G1 and G2, with marked spatial segregation but occasional geographic adjacency of different groups, as well as moderate genetic differentiation ($F_{ST} = 0.2012$) coupled with distinct levels of genetic diversity between groups (higher heterozygosity, allelic richness and amount of private alleles in G1). These results are consistent with a scenario of multiple independent introductions, which would be at least two in the studied basin, composed of genetically diverse propagules during the initial colonization. These introductions appear to have remained largely genetically isolated, producing a patchwork of genetic groups (still) without interbreeding. Spatially aggregated genetic groups (a phenomenon known as genetic patchiness), often comprising mostly full and

half-siblings, have also been observed in other plant species within their native ranges (e.g., *Quercus robur* in Finland; Vakkari et al. 2020). In the invasive *P. angustifolia*, kinship analyses revealed extensive familial relationships confined within genetic groups, with first-degree relatives predominating in G1 and a more mixed pattern in G2, including second- and third-degree relatives as well as some unrelated individuals. The absence of kinship relationships between groups further supports their independent origins and the absence of post-establishment intermixing. Moreover, a significant but weak positive IBD pattern detected after controlling for kinship suggests that genetic similarity decreases with geographic distance across the landscape, likely reflecting limited gene flow and spatial clustering among genetic groups. The genetic structure observed would be therefore due to the introduction of different genetic groups and family ties between most individuals.

Colonization bottlenecks are expected to reduce genetic variation, with theory predicting a decay in heterozygosity following sudden reductions of population size (Nei et al. 1975; Allendorf and Leary 1986). This trend is defied by invasive species and their success despite these challenges has been described as a ‘genetic paradox’ (Allendorf and Lundquist 2003; Schrieber and Lachmuth 2017). The case of *P. angustifolia* presents an additional oddity, given that the negative inbreeding coefficients (F_{is}) and higher H_o than H_e indicate an excess of heterozygosity in both genetic groups. This apparent contradiction with what is expected in a self-compatible and self-pollinating species may be explained by the persistence of heterozygosity inherited from heterozygous founders, which has not yet been eroded by genetic drift, particularly if the invasion is recent. The naturalization of the species in the country, documented just over 30 years ago (Jocou and Gandullo 2019), suggests that the invasion of *P. angustifolia* is indeed recent. This is consistent with the historical knowledge as recounted by local residents during our interviews and informal conversations (pers. obs.). The unexpectedly high heterozygosity observed in *P. angustifolia* could be explained by several other factors. Excess heterozygosity may also be a transient outcome of recent population bottlenecks combined with the absence of random mating. For instance, analyses of isolated populations of animals with known origin and founder group composition have detected high heterozygosity, which was considered to be expected in the first generations following a founder event with a small number of individuals and in the absence of random mating (Blanco et al. 2021; Kekkonen et al. 2012). Another possibility is selection favoring heterozygosity itself that may contribute to maintaining genetic diversity in selfing populations (e.g., Pemberton et al. 1996). It is important to remember that invasive populations consist of individuals (and their descendants) that have successfully persisted through the early stages of invasion, which function as a selective filter, in particular the establishment phase. Given these complexities and the lack of direct studies on *P. angustifolia* in its native range, and since the origin and the initial production of propagules introduced in Córdoba for this species are unknown, further research into its genetic diversity and population genetics is required to clarify the mechanisms underlying the observed singularity.

The presence of two distinct genetic groups with different kinship relationships composition can be explained by either asynchronous introductions, where G2 was introduced earlier, allowing more generations of local recruitment, or by differences in the sources and kinship composition of each introduction, with G1

founded by siblings and/or parents-offsprings and G2 originating from a more mixed family group (and not all family members). The close kinship relations observed throughout the sampled area suggesting strong family structuring could also indicate recent colonization events involving a limited number of founding individuals, consistent with expectations for invasive species. We recall here once again that the naturalization of the species spans only a few decades (Jocou and Gandullo 2019), which would account for our findings. As in any expanding population, genetic patterns are expected to shift over time, and similarly, the kinship structure is also expected to evolve as generational turnover accumulates. With ongoing invasion, genetic drift and continued inbreeding are likely to cause a gradual loss of heterozygosity and an increase in the inbreeding coefficient. However, in our case study, as family patches continue to expand, contact and mixing between the two genetic groups may occur and thereby the trend could change. New genotypes may be generated, increasing heterozygosity and potentially altering the future trajectory and dynamics of the invasion. Post-introduction admixture has been proposed to enhance invasiveness by increasing genetic diversity and helping invaders overcome founding effects (Smith et al. 2020; Tang et al. 2022; McCulloch et al. 2023). It has also been recorded that it generates novel genetic variants (e.g., Vallejo-Marín et al. 2020) and increases genetic diversity that improves fitness (e.g., Ollivier et al. 2020). The future trajectory of the invasion of *P. angustifolia* in the studied area remains uncertain and will partly depend on the management actions undertaken (see Final Remarks section).

One possible explanation for the high proportions of kin pairs within sites and short distances is recruitment pulses involving related individuals (Iacchei et al. 2013). The estimated dispersion kernels, that use information from kinship relationships, suggest a dispersion pattern characterized by short-distance movements with occasional longer-range dispersal events in *P. angustifolia*, both when analyzing the complete sampling and when analyzing only the samples within the basin. The convergence of kinship relationships of varying degrees across different collection sites, as revealed by network mapping, along with the presence of kin pairs spanning the full range of spatial distances, implies overlapping generations at multiple locations across the basin. This pattern underscores the prevalence of short-distance dispersal, leading to the concentration of successive generations within these same sites. Integrating all the evidence allows us to hypothesize invasion dynamics, for both genetic groups, characterized by extensive local recruitment and family expansion at each site, generational overlap, and occasional but significant long-distance dispersal, resulting in a highly kin-connected population throughout the invaded basin. The hypothesized dynamics and pathways of *P. angustifolia* invasion can be better understood by considering the reproductive biology and dispersal mechanisms of the species. As a self-compatible shrub capable of producing high fruit yields through self-pollination (pers. obs.), *P. angustifolia* can establish and reproduce even under conditions of low density. Such autonomous reproduction is a common trait among successful colonizer plants, promoting rapid expansion and persistence in new environments (Razanajatovo et al. 2016). Local recruitment and seed dispersal via native frugivorous birds (mainly genus *Turdus*; Vergara-Tabares et al. 2016) likely foster family group expansion within genetic clusters of *P. angustifolia*. Although previous findings indicate that most of *P. angustifolia* seeds are dispersed at short distance (Vergara-Tabares 2017), our results highlight that long-distance seed dispersal events also play a key role in the advance of invasion.

These seed-dispersing birds are capable of traveling longer distances but seed retention times are low (Bracho-Estévez et al. 2024), suggesting that long-distance seed dispersal may be exerted by other animals such as mammals (we discard pigeons and parrots because they predate *P. angustifolia* seeds; Herrera-Simó et al. 2024; De Luca et al. 2025).

Final Remarks

Our findings support the hypothesis that invasion dynamics of *P. angustifolia* in the studied Chaco Serrano basin are shaped by a spatially explicit genetic structure, driven by its reproductive biology and predominantly short-distance dispersal. However, effective long-distance dispersal events substantially contribute to range expansion, resulting in a complex invasion mosaic. Because plant density declines with distance from the urban area, which acts as the primary invasion source, individuals located farther away represent the advancing invasion front. These peripheral plants are critical for the invasion control, as fruiting adults can produce millions of seeds, ensuring continued spread if left unmanaged. The combined evidence has direct management implications. When resources are limited, control efforts should prioritize removal of isolated or distant individuals at the invasion front, where interventions are most effective at preventing further spread. With additional resources, management can be expanded to include individuals in densely invaded sectors, with particular surveillance along watercourses. In addition, because the species spreads as family groups over both short and long distances, management should not be limited to single focal points, as any plant/patch can become a source of new propagules, capable of bridging both distance ranges. As a general rule, control measures should also seek to prevent admixture between kin-structured genetic groups. The evidence of multiple introductions in this confined area highlights the importance of monitoring isolated plants, identifying additional propagule sources, and preventing further introductions. The control method shown to impair flowering and fruiting (Fernández et al. 2024) should be finetuned and implemented with these dispersal dynamics in mind. Overall, our study demonstrates how fine-scale spatial and genetic analyses can guide optimized, tiered management strategies to improve control actions and reduce the spread of invasive species in affected ecosystems.

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Author Contributions

All authors contributed to the study conception, design, and interpretation of the results. Data and sample collection were performed by LF and CCG. Lab work was done by CCG. Formal analysis was done by LF and CCG. The first draft of the manuscript was written by CCG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability

The data that supports the findings of this study are available within the manuscript and its Supplementary Information file. Raw sequencing data are available from the authors upon request.

Declarations

Conflict of Interests

The authors declare no conflict of interest.

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