



Hybridization, ecological niche, and conservation of the threatened endemic species *Limonium esteveei*: an integrated approach in the genus *Limonium*

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Abstract

Hybridization between widespread species and narrow endemics poses a serious conservation threat, often leading to extinction via genetic swamping. In this study, we applied an integrated approach—combining genetics, morphometrics, and functional ecology—to investigate the implications of hybridization between the widespread species *Limonium cossonianum* and the Critically Endangered *L. esteveei*. We combined molecular markers (AFLPs, ITS, and chloroplast markers), morphometric analyses, and elemental profiling of leaves and soils. Elemental profiles provided a novel proxy for biogeochemical niche differentiation, while genetic markers resolved phylogenetic relationships and the direction and extent of gene flow. Crucially, our results revealed extensive and asymmetric introgression occurring exclusively from the hybrid into *L. cossonianum*, with no evidence of genetic swamping affecting the genetic integrity of *L. esteveei*. Elementome analyses showed that *L. cossonianum* occupies a significantly distinct biogeochemical niche, whereas *L. esteveei* and the hybrid share similar elemental composition. Furthermore, the hybrid's elementome exhibited a mosaic inheritance pattern, suggesting a novel functional strategy that may contribute to its local persistence. We conclude that the mechanisms of niche differentiation, coupled with reproductive asymmetry, have acted as an evolutionary shield for *L. esteveei*, protecting this species from extinction through genetic swamping. Our findings indicate that, although hybridization does not currently threaten the genetic integrity of *L. esteveei*, its long-term persistence will depend on the conservation of the highly specific edaphic conditions on which the species relies. Given the marked soil specialization documented here, strategies focusing on the preservation of its functional and edaphic niche are likely to be essential.

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Keywords Edaphic specialization · Genetic swamping · Hybridization · Saline soils · Threatened endemism

Introduction

Limonium Mill. is the most extensive genus within family Plumbaginaceae Juss., encompassing 608 species (Plants of the World Online [POWO] 2025) of therophytes, perennial herbs and small shrubs of ornamental interest. These species often colonize minor and isolated areas, particularly those with saline (seaside cliffs, salt marshes, etc.), gypsum or arid substrates, exhibiting a primary diversification center in the Western Mediterranean region and another in the Asian steppes (Erben 1990).

The diversity and complexity observed within this genus can largely be attributed to hybridization (Erben 1990; Palacios et al. 2000), a phenomenon known to function as a powerful evolutionary driver by enhancing fitness (Brochmann et al. 2004). This remarkable hybridization capacity becomes particularly evident when examining the number of *Limonium* hybrids recorded in plant databases. According to POWO (2025), there are 14 currently accepted hybrids in the Iberian Peninsula, although more than 140 have been documented in *Flora iberica* (Erben 1990). Further evidence of this capacity is the frequent occurrence of species that hybridize with multiple congeners. A case in point is *Limonium cossonianum* Kuntze, an Iberian endemism distributed along the Spanish Levantine coast, Granada, Albacete and the Balearic Islands, which can hybridize with up to six other *Limonium* species. One such is *Limonium estevei* (Fernández-Casas 1971), a critically endangered (CR, B1ab(iii,v)+B2ab(iii,v); Mota et al. 2004; Mendoza-Fernández et al. 2019) narrow endemic, with which *L. cossonianum* coexists in a sympatric manner in Playa Maceñas (Mojácar, Almería). In this locality, individuals exhibiting apparently intermediate morphological traits are frequently observed (Fig. 1a). This can be explained by sympatry, along with other shared factors like identical chromosome numbers ($2n=16$; Ingrouille 1984), overlapping flowering periods (Mota et al. 2004), and sexual reproduction, all of which promote the emergence of hybrids between both species (Erben 1978, 1990).

The presence of these hybrids raises a previously recognized but underexplored concern for *L. estevei*, in addition to the intense anthropogenic pressure threatening its habitat (Mota et al. 1999, 2004). Hybridization between a widespread taxon and a locally rare endemic (i.e. *L. cossonianum* and *L. estevei*), followed by repeated backcrossing and introgression, can have major evolutionary consequences (Hegde et al. 2006; Gómez et al. 2015). This process may lead to the replacement of the rare species due to genetic swamping, where gene flow from the more abundant species overwhelms the gene pool of the rarer one (Goulet et al. 2017). If such a process occurs between the hybrid and *L. estevei*, it could compromise the genetic integrity of the latter and pose a serious extinction risk for this already critically threatened endemic (Mota et al. 1999, 2004; Rodríguez-Tamayo et al. 2003). This scenario also invites to consider the long-term effects of introgressive hybridization and the potential for genetic assimilation of rare genotypes into more widespread lineages.

In light of these potential detrimental consequences, the accurate identification of hybrid individuals is a crucial first step in assessing the conservation risks faced by *L. estevei* population. Traditionally, hybrid identification has relied solely on the recognition of the intermediate morphology of hybrids compared to their parental species. However, this approach

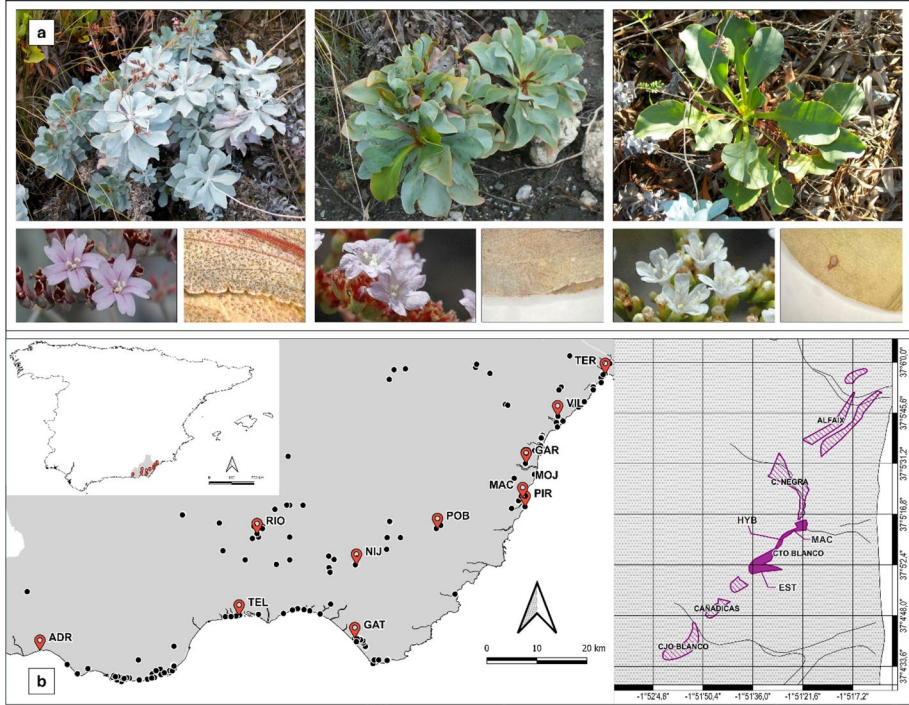


Fig. 1 **a** Most distinctive qualitative morphological traits between *L. estevei* Fern. Casas (left) and *L. cossonianum* Kuntze (right), which appear to be intermediate in the hybrid (center). *L. estevei*: leaves oblanceolate-spatulate, bluish green with white speckles, highly undulated margins, arranged in a dense helicoidal pattern; petals pale violet. *L. cossonianum*: leaves elliptic-ovate, green, with entire margins, arranged in basal rosette; petals white. **Hybrid**: leaves resembling those of *L. cossonianum*, blue green to olive green, with undulated margins, arranged in a spiral pattern as in *L. estevei*; petals whitish violet. **b** Distribution maps. Left: sampling sites of *L. cossonianum* in the province of Almería; black dots indicate the species' distribution area. Right: locality of Macenas. Purple grids indicate the area of presence of *L. estevei* (eight subpopulations). The solid-colored grid represents the study area where EST, MAC and HYB samples were collected. Population codes correspond to those listed in Table 1

presents several challenges. On the one hand, *Limonium* represents a taxonomically complex genus, with species that often exhibit morphological characteristics so similar that morphometric analyses alone are insufficient to achieve an accurate species-level identification. Nonetheless, in the case under study, both parental species exhibit clear differences in vegetative and reproductive characters (Table S1), and hybrid individuals apparently show intermediate traits, suggesting that morphometric analysis could provide useful insights. Even so, morphological intermediacy as an indicator of hybrid ancestry remains problematic, since it may result from phenotypic plasticity, correlated traits, or other processes unrelated to hybridization (Urfus et al. 2025). Thus, given these challenges, the most reliable strategy for hybrid identification consists in the integration of morphological and molecular data, a common practice across diverse gymnosperms (*Pinus* L., Jasinska et al. 2010) and angiosperms genera (*Anthoxanthum* L., Pimentel et al. 2010; *Centaurea* L., Ferriol et al. 2012; *Limonium* Mill., Rodríguez et al. 2003; Iamónico et al. 2022; *Populus* L., Deacon et al. 2017).

In particular, the molecular component of this strategy relies on the use of different genetic markers. For instance, AFLPs (Vos et al. 1995) have been widely used in angiosperm hybridization studies to decipher the hybrid origin of many taxa by correlating their genetic patterns with those of parental donors (Han et al. 2000; Marhold et al. 2002; Segarra-Moragues et al. 2007). The ribosomal ITS region enables the identification of interspecific hybrids through the detection of ribotypes inherited from the parental species (Aguilar et al. 1999; Baldwin et al. 1995). Plastid DNA markers are also commonly used to trace maternal lineages (Corriveau and Coleman 1988). Together, these markers have been widely applied in the genus *Limonium* to resolve species boundaries, detect hybridization events, and reconstruct phylogeographic patterns (Lledó et al. 2005; Malekmohammadi et al. 2017; Koutroumpa et al. 2018).

Turning to another aspect, beyond morphometrics and genetics, understanding the potential ecological consequences of hybridization for *L. estevei* requires examining biogeochemical niches segregation/overlap. Such analyses provide insight into the extent to which hybrids can occupy the parental species' microhabitats. In this regard, Peñuelas et al. (2019) highlight that two species coexisting in sympatry tend to show different contents of all (or at least most) bioelements (elementomes), reflecting their evolution towards distinct life strategies and an attempt to mitigate competitive pressure. A substantial divergence between elementomes would thus indicate the occupation of different biogeochemical niches (Fernández-Martínez 2021). In the specific case of *L. estevei* and *L. cossonianum*, although inhabiting the same area, they seem to show completely different niche preferences: while the local endemism thrives on craggy ground, *L. cossonianum* predominates in a sandy depression. Thus, the initial approach would be to assess whether the two populations of *Limonium* in Macenas meet these criteria, displaying divergent elementomes and biogeochemical niches. The information obtained could also elucidate the hybridization event, particularly if the hybrid shows an intermediate elemental profile compared to that of the parental species.

The main goal of this study was to evaluate hybridization between the Critically Endangered *Limonium estevei* and the widespread *L. cossonianum* in Playa Macenas and to assess its implications for the conservation of *L. estevei*. Specifically, we aimed to:

Characterize the genetic and morphological relationships among *L. estevei*, *L. cossonianum* and the hybrid individuals in order to determine the presence, extent and direction of hybridization and introgression.

Assess edaphic and biogeochemical niche differentiation among the three taxa to evaluate whether ecological segregation reduces hybridization risks for *L. estevei*.

Integrate genetic, morphological and ecological evidence to determine whether hybridization represents a conservation threat to *L. estevei* and to inform evidence-based recommendations for its in situ management.

Methods

Study area and sampling

The study area (Fig. 1b) focused on Macenas (Mojácar, Almería), a coastal locality included in the Site of Community Importance (SCI) of Sierra de Cabrera-Bédar (ES6110005), in

the southeastern Iberian Peninsula. Within this area, the two target species (*L. cossonianum* and *L. estevei*) exhibit a sympatric distribution, with individuals often growing only a few meters apart. These species are characteristic components of the habitat of community interest ‘Mediterranean salt steppes’ (Natura 2000 code 1510).

For molecular analyses, fresh leaves of 14 *L. estevei*, 10 *L. cossonianum* and 13 hybrid individuals identified in Playa Macenas were collected and dried in Silica Gel (Chase and Hills 1991). To ensure appropriate coverage of the distribution and geographic diversity of *L. cossonianum*, 55 individuals from 11 further localities were similarly sampled (Fig. 1b and Table 1). Complete specimens were also collected to prepare vouchers intended for morphometric analyses (Table S2).

For elemental composition analyses, leaf samples from five *L. cossonianum*, five *L. estevei*, and five hybrids from Playa Macenas were gathered. Additionally, soil samples associated with these individuals and five control soils (outside the canopy of any target plant) were collected. Both foliar and soil samples were processed and analyzed as described in the following sections to obtain their elemental composition. Detailed information about the study area and sampling is provided in Appendix A2.1.

DNA extraction and AFLP analysis

Genomic DNA was extracted from dried leaves of the 82 sampled individuals (55 *L. cossonianum*, 14 *L. estevei* and 13 hybrids). DNA quality was checked via gel electrophoresis and fluorometric quantification prior to use in molecular analyses, including AFLP fingerprinting and the amplification of nuclear (ITS) and plastid markers (*matK*, *rbcL*, *trnL-F*; see Appendix A2.2).

Amplified Fragment Length Polymorphism (AFLP) analyses followed the protocol of Vos et al. (1995), with modifications. Genetic distances were calculated based on presence/absence matrices (Appendix B1) using Dice (1945) and Jaccard (1908) similarity coefficients. Reticulate genetic patterns potentially indicative of hybridization were explored with a NeighbourNet analysis (Bryant and Moulton 2004) implemented in SplitsTree4 (Huson and Bryant 2006). To assess genetic structure and detect hybridization events, a Bayesian clustering approach was employed using STRUCTURE v2.3 (Pritchard et al. 2000; Falush et al. 2003, 2007). Further details about the protocol, marker selection, software parameters, and reproducibility thresholds are provided in Appendix A2.2.

Nuclear ribosomal and plastid DNA amplification and sequencing

DNA extracted from five *L. estevei*, five hybrid and twenty *L. cossonianum* individuals (Table S2) was used as a template to amplify one nuclear (ITS) and three plastid regions (*matK*, *rbcL* and *trnL-F*) using published universal primers (Taberlet et al. 1991; Lledó et al. 1998; Ford et al. 2009; Cheng et al. 2016). PCR products were sequenced using Big-Dye chemistry on an ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems), and raw chromatograms were edited and aligned in Geneious Pro v4.8.5 (Kearse et al. 2012; see Appendix A2.3).

Additive polymorphic sites (APS), corresponding to overlapping peaks in ITS chromatograms, were identified and coded using IUPAC ambiguity symbols (Aguilar et al. 1999). To resolve ribotype structure and identify hybrid signatures, cloned ITS sequences were

Table 1 Localities sampled of *Limonium estevei*, *L. cossonianum* and the hybrid, including population codes used in the text and figures and coordinates in DMS

Species name	Popula- tion code	Locality	Latitude	Longitude	Indiv. analysed	No. Poly. frags	No. Fix. poly	Tifrag	%Pol	He	No. Priv. frags
<i>L. cossonianum</i>	MAC	Macenas	37°05'13"N	1°51'20"W	10	33	127	160	0.10	0.05	3
	PIR	Torre del Pirulico	37°45'52658"N	1°51'2.62588"W	5	19	128	147	0.06	0.03	2
	MOJ	Mojácar	37°9'49.79566"N	1°50'55.52169"W	5	33	122	155	0.10	0.06	10(3)
	GAR	Garnucha	37°9'46.25432"N	1°50'54.90164"W	5	40	123	163	0.13	0.07	4
	VIL	Villaricos	37°15'59.97163"N	1°46'40.49647"W	5	26	121	147	0.08	0.04	2
	TER	San Juan de los Terremos	37°21'36.08669"N	1°40'15.65730"W	5	32	124	156	0.10	0.06	3
	POB	Venta del Pobre	37°17'71559"N	2°2'52.39049"W	5	34	123	157	0.11	0.06	1
	TEL	San Telmo	36°49'42.65793"N	2°29'37.42119"W	5	32	117	149	0.10	0.06	3
	NIJ	Níjar	36°56'24.91980"N	2°13'48.01385"W	5	24	118	142	0.08	0.04	5(3)
	GAT	Cabo de Gata	36°46'43.79510"N	2°14'1.44703"W	5	20	128	148	0.06	0.04	3(1)
Putative hybrid <i>L. estevei</i>	ADR	Adra	36°45'4.12521"N	2°56'28.76941"W	0	—	—	—	—	—	—
	RIO	Rioja	37°027.12653"N	2°27'12.09784"W	0	—	—	—	—	—	—
					55	153	88 (23)	241	0.48	0.12	71
						(121)					
	HYB	Macenas	37°05'09"N	1°51'26"W	13	61	181	242	0.19	0.07	0
	EST	Macenas	37°05'04"N	1°51'31"W	14	26 (15)	151	177	0.08	0.02	6
							(65)				
	Total					82	259	62			

AFLP-derived parameters are also shown: number of polymorphic (No. Poly. frags) and fixed fragments (No. Fix. frags), total number of fragments (Tifrag), percentage of polymorphic fragments (%pol), expected heterozygosity (He) and number of private fragments (No. Priv. frags.). Values in parentheses represent the number of taxon-specific fragments, excluding hybrids. AFLP data for ADR and RIO are not available, as these localities were included only in the ITS analysis

obtained from selected individuals representing both parental species and hybrids (Appendix A2.4; Table S2). A NeighbourNet was constructed based on direct and cloned ITS sequences (see Appendices B2 and B3) using SplitsTree 6 (Huson and Bryant 2006), a particularly well-suited method for visualizing reticulated patterns associated with hybridization (Bryant and Moulton 2004).

Morphometric analysis

Fifty-nine vouchers, including six from the locus classicus of *L. cossonianum*, were subjected to an exhaustive morphological assessment. For each of the 34 selected quantitative characters (four discrete and thirty continuous; Table 2), five measurements were taken using a digital caliper and a stereomicroscope (EZ4 W; Leica Microsystems, Wetzlar, Germany). Recorded images were processed and analyzed in ImageJ 1.53t (Schneider et al. 2012), following the guidelines described in Appendix A2.5.

The data matrix of 9086 values (Appendix B4) was first normalized by dividing each variable by its standard deviation. A Principal Component Analysis (using PAST 4.13; Hammer et al. 2001) was then conducted to reduce its dimensionality. Results were visualized in two-dimensional scatter plots, allowing for a comprehensive evaluation of morphological variability both within and among groups (Ringnér 2008). Statistical support for this analysis was provided through a one-way ANOVA, with significance set at $p < 0.05$ (Statgraphics v.19.4.04; Statgraphics Technologies Inc. 2022).

Edaphic properties and elemental analyses

Soil and leaf samples from five *L. estevei*, five *L. cossonianum*, five hybrid individuals, and control sites from Playa Macenas were analyzed to characterize edaphic conditions and elemental composition. Leaf and soil total/phytoavailable elemental profiles were quantified using ICP-OES (Jiménez-Heinert et al. 2020) and an Elemental Analyzer at the Ionomics Laboratory of CEBAS-CSIC. Phytoavailable fraction was extracted following Quevauviller et al. (1997), with EDTA efficiency supported by Abedin et al. (2012) and Merlo et al. (2021). Essential nutrients were selected according to Barker and Pilbeam (2015), with the inclusion of Na and Sr due to their ecological significance. Detailed protocols, datamatrices and parameters used in statistical analyses are described in Appendices A2.6 and B5-B11.

Results

AFLP analysis

The AFLP analysis (2.54% error rate) generated 321 bands from three primer combinations (Table 1), enabling the identification of a unique AFLP phenotype for each sample. These primers amplified 241 bands in *L. cossonianum* and 177 in *L. estevei*, with 144 and 80 exclusive to each species, respectively, and 97 shared by both taxa. The same combination of primers produced 242 bands in the 13 hybrid samples; all present in at least one parental individual. Low-frequency bands unique to *Limonium* sp., absent in hybrids, were discarded.

Table 2 List of measured quantitative morphological characters, with their corresponding units and acronyms used in text and figures

No.	Morphological character	Acronym	Unit
1	Plant height	H	mm
2	Length of the leaf	LL	mm
3	Length of the blade	BL	mm
4	Width of the blade	BW	mm
5	Length of the petiole	PL	mm
6	Width of the petiole	PW	mm
7	Number of lateral veins*	NLV	–
8	Number of floral scapes*	FSN	–
9	Length of the floral scape	FSL	mm
10	Branching starting point	BSP	mm
11	Maximum length of the first-order branches	FBL	mm
12	Average angle between branches	BAA	°
13	Length of the spike	SPL	mm
14	Maximum distance between spikelets	SKG	mm
15	Number of spikelets per spike*	SKN	–
16	Number of spikelets per cm*	SKD	–
17	Length of the spikelet	SKL	mm
18	Length of the outer bract	OBL	mm
19	Width of the outer bract	OBW	mm
20	Length of the median bract	MBL	mm
21	Width of the median bract	MBW	mm
22	Length of the inner bract	IBL	mm
23	Width of the inner bract	IBW	mm
24	Length of the inner bract central section	IBCL	mm
25	Width of the inner bract central section	IBCW	mm
26	Width of the inner bract margin	IBM	mm
27	Length of the inner bract apex	IBAL	mm
28	Length of the calyx exceeding the inner bract	CAIB	mm
29	Length of the bracteoles	BRL	mm
30	Length of the calyx	CL	mm
31	Length of the calyx tube	TL	mm
32	Length of the calyx limb	CLL	mm
33	Length of the calyx teeth	CTL	mm
34	Width of the calyx teeth	CTW	mm

Discrete characters are indicated with an asterisk (*)

The percentage of polymorphic fragments was strongly correlated with the per-population diversity index (He; Spearman's $r_s = 0.913$, $p < 0.0001$). Both indices were significantly higher in hybrids than in parental individuals (Mann–Whitney U-test). No significant differences in genetic diversity were observed among populations of *L. cossonianum* potentially affected by hybridization compared to other populations, although values were slightly higher in Macenas.

The NeighbourNet constructed with AFLP phenotypes revealed the intermediate genetic character of the hybrids with respect to those of the parental taxa (Fig. 2a). Samples of *L. estevei* formed a well-defined cluster at the right end of the network, while those of *L. cossonianum* were grouped at the opposite end, and the 13 hybrid samples were in an intermediate position between these two clusters (though closer to *L. estevei*).

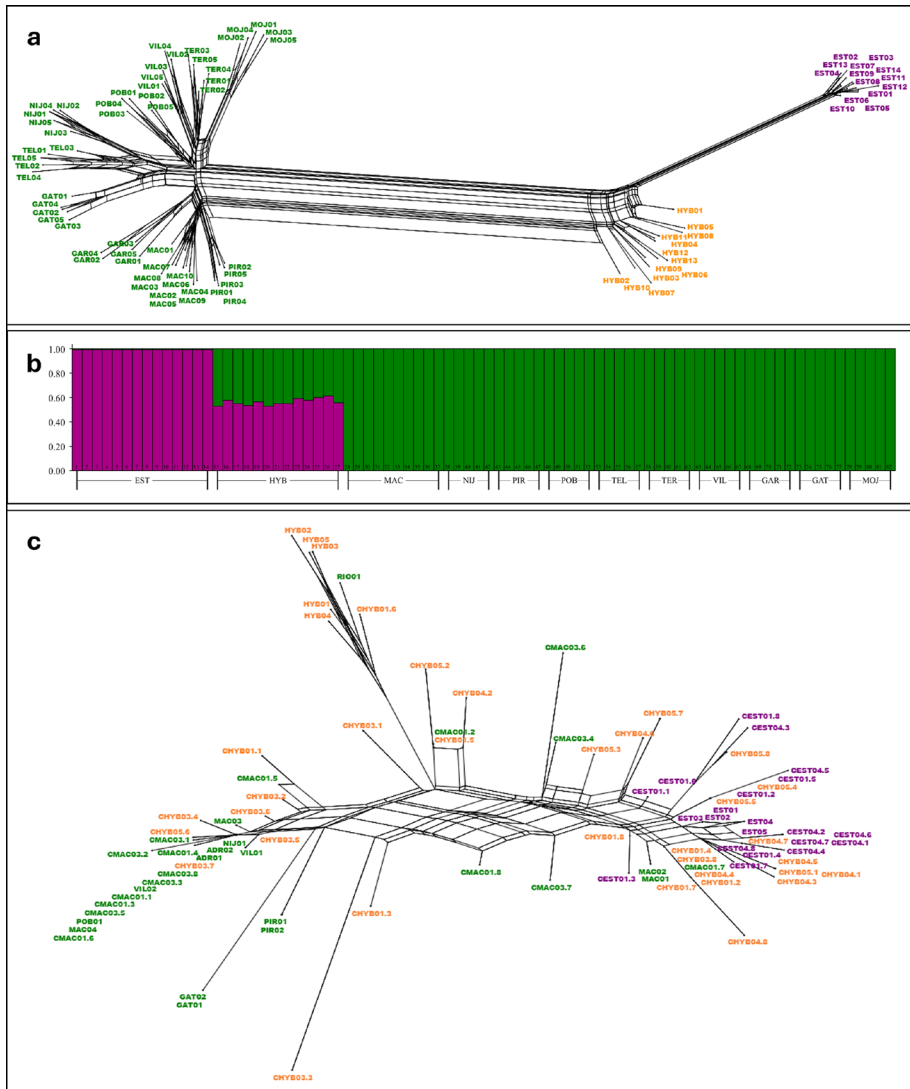


Fig. 2 **a** NeighbourNet based on AFLP phenotypes of the 82 individuals studied: 55 *L. cossonianum* (10 from MAC and 5 from each of the 9 further localities within its distribution range: PIR, MOJ, GAR, VIL, TER, POB, TEL, NIJ and GAT), 14 *L. estevei* (EST) and 13 hybrids (HYB). **b** Proportional assignment of the 82 individuals of *L. cossonianum*, *L. estevei* and hybrids to genetic groups I (green) and II (purple), as identified in an admixture analysis using correlated allele frequencies from AFLP data. **c** NeighbourNet based on ribosomal sequences obtained through direct sequencing and cloning. Clones are labeled as “C+population code”. Samples of *L. cossonianum*, *L. estevei* and the hybrid are represented in green, purple and orange, respectively. Population codes correspond to those listed in Table 1

Bayesian analysis showed some degree of differentiation in our molecular dataset (Fig. 2b). The optimal number of groups was $K=2$ ($-\ln(P)=-7265.98$), corresponding to *L. estevei* and *L. cossonianum*. A certain admixture component was found in samples of hybrid origin, with approximately half of their membership assigned to each parental group.

Nuclear ribosomal and plastid DNA analysis

Ribosomal sequences obtained through direct sequencing had lengths of 692 and 693 bp in *L. estevei* and *L. cossonianum*, respectively. The alignment of these sequences revealed 16 additive polymorphic sites, most of them positioned in the internal transcribed spacers (eight in ITS1 and six in ITS2). The APS included both differential positions between the two potential parent species and intraspecific polymorphisms (237, 258 and 653 from *L. estevei* and 439 from *L. cossonianum*). Samples of hybrid origin exhibited additivities at all the identified positions, whereas in *L. cossonianum* samples from Macenas, at least six of these sites were found. Results are summarized in Table S3.

The inclusion of the 64 clones into the previous alignment led to an increase in the number of variable sites. However, since all of them were non-informative, either representing point mutations observed in a single clone or nucleotide substitutions absent in the presumed parental species and not occurring in more than two clones, they were excluded when defining the ribotypes. Twenty different ribotypes were identified (see Table S4).

In the NeighbourNet (Fig. 2c), sequences of *L. estevei* formed a well-defined cluster at one end of the network, while *L. cossonianum* ones were mainly grouped at the opposite end. The direct sequences of the hybrid samples occupied an intermediate position, and most of its clones were resolved within the parental clusters, although some appeared dispersed across the network.

Plastid markers sequences' length was 823 bp for *matK*, 893 bp for *trnL-F* and 1218 bp for *rbcL*. A single polymorphism was identified in the *matK* gene of the Macenas individuals. While *L. cossonianum* and *L. estevei* exhibited a T at position 453, the hybrid showed either a T or G. The other two amplified regions, *trnL-F* and *rbcL*, were identical in all the individuals from this locality. However, another polymorphism was detected in sequences from ADR, GAR, POB, TEL, TER and VIL, which carried a G at position 379 of the *rbcL* gene, in contrast to the A found in the Macenas samples.

Morphometric analysis

Given the large number of variables ($p=34$) and observations ($n=59$), a variance threshold of 60% was adopted (Jolliffe 2002), retaining three meaningful components in the PCA ($PC1=35.69\%$, $PC2=15.82\%$, and $PC3=9.28\%$). In the two-dimensional scatter plots obtained (Fig. 3a), samples of *L. estevei* were clustered at the positive end of the x-axis, while those of *L. cossonianum* from Macenas were grouped at the opposite end, encompassed within the dot cloud corresponding to samples covering the species' distribution range. Hybrid individuals were once again positioned in-between the clusters of the two parent species.

Specimens of *L. estevei* exhibited longer spikes and spikelets, as well as larger bracts, bracteoles and calyces. In contrast, individuals of *L. cossonianum* had larger leaves with thinner petioles and a greater number of lateral veins. Hybrids displayed a floral morphol-

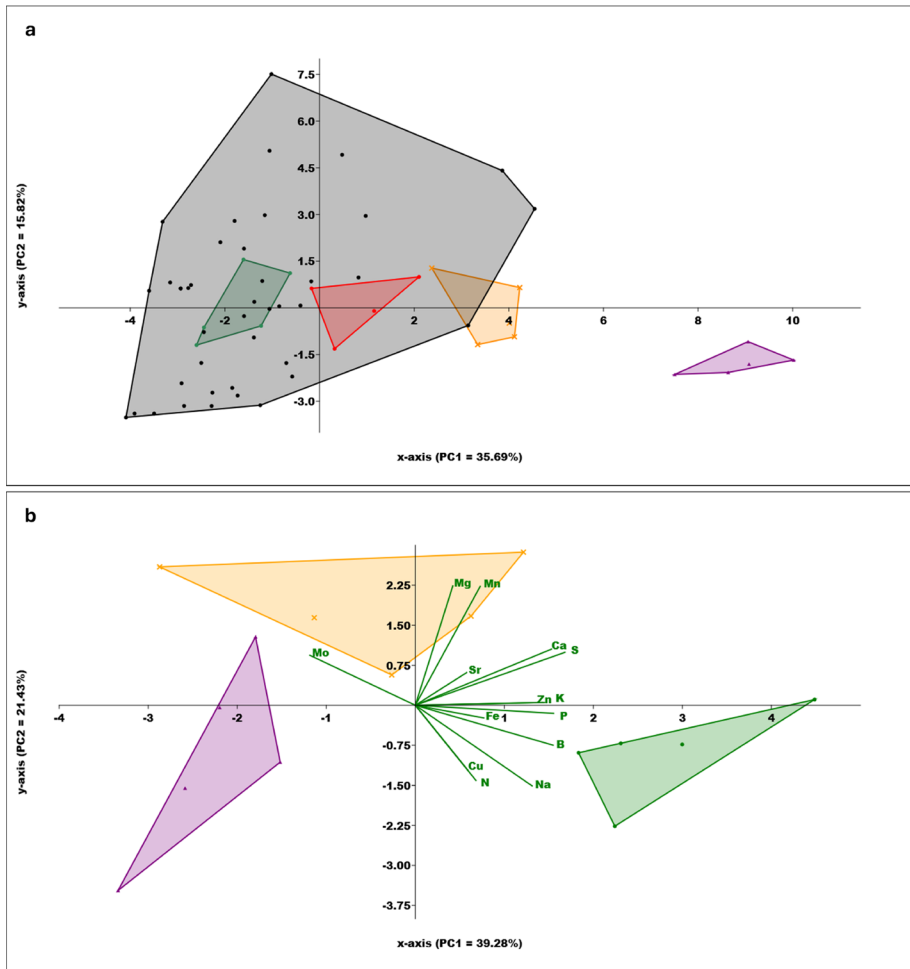


Fig. 3 Scatter plots representing the first two components of the Principal Component Analysis conducted on **a** the 34 quantitative morphological characters and **b** foliar concentrations of essential macro and micronutrients (N, P, K, Ca, Mg, S, B, Cu, Fe, Mn, Mo and Zn), Na and Sr. Colored convex hulls highlight clusters with significantly distinct centroids (statistical support provided in Table S5 and S12, respectively): green=*L. cossonianum* from Macenas (MAC), purple=*L. estevei* (EST), orange=hybrids (HYB), red=*L. cossonianum* from the holotype locality (GAT), and grey=*L. cossonianum* from further localities across the species' distribution range (ADR, GAR, GAT, NIJ, PIR, POB, RIO, TEL, TER and VIL). Population codes correspond to those in Table 1

ogy and certain foliar traits (e.g. number of lateral veins) intermediate to that of the parental species, but their foliar architecture in terms of blade length and petiole dimensions (length and width), bore a close resemblance to that of *L. cossonianum*.

Among the 34 characters measured in hybrids, eleven were directly inherited from one of the parental species (four from *L. estevei*, seven from *L. cossonianum*), twelve were intermediate and two transgressive. The remaining nine characters were considered non-diagnostic due to the absence of significant differentiation across taxa (ANOVA, $p < 0.05$;

Table S6). After excluding these, the proportional distribution of trait types was: 44% parental, 48% intermediate and 8% transgressive.

Edaphic properties and elemental analyses

Bayesian ANOVA revealed significant differences in pH ($p=0.003$) and electrical conductivity (EC; $p<0.001$) among the four soil types (Table S7), with *L. estevei* soils being the most alkaline ($\bar{x}=10.26$) and controls showing the lowest EC values ($\bar{x}=0.205$ dS/m), as supported by moderate to strong post hoc evidence.

Soils associated with the studied taxa exhibited low total N and P and high Na levels (Table 3; Table S8). PERMANOVA revealed significant differences in total soil composition among microhabitats ($F=1.954$; $p=0.038$), attributed to the divergence between control and *L. estevei* soils ($p=0.015$). Pairwise comparisons indicated that control soils were more closely related to those of *L. cossonianum* ($p=0.2692$), whereas hybrid ones were more similar to those of *L. estevei* ($p=0.8475$; Table S9). Although PCA did not clearly separate clusters (Figure S1a), their spatial distribution was consistent with these patterns.

In the phytoavailable fraction, only P and Mg varied significantly among soils (Table 3; Table S10), with hybrid-associated soils showing intermediate concentrations relative to the parental taxa. Na was consistently higher in all plant-associated soils compared to controls. In the scatter-plot (Figure S1b), control soils were separated from plant-associated ones along the x-axis, a pattern supported by PERMANOVA ($p=0.009$, 0.0103, and 0.008 for CTRL vs MAC, EST, and HYB, respectively; Table S9). Soils under *L. estevei* and *L. cossonianum* also diverged along this axis ($p=0.04$), while hybrid-associated soils occupied an intermediate, partially overlapping position.

Differential concentrations of nearly all foliar macro- and micronutrients were also observed among the three taxa (Table 4; Table S11). C was found at higher concentrations in leaves of *L. estevei*, while Na was present at much higher levels in *L. cossonianum* ones. The distribution of groups in the scatter-plot (Fig. 3b) suggests that secondary macronutrients have a stronger influence than primary macronutrients on ecological niche differentiation.

Discussion

Genetic and morphological characterization: hybridization, recombination and introgression

The results of genetic and morphological analyses have provided clear evidence for distinguishing the hybridization event between *L. cossonianum* and *L. estevei*. In the STRUCTURE analysis ($K=2$) based on AFLP data (Fig. 2b), all hybrids were inferred to be of admixed origin, exhibiting approximately equal genetic assignment (~50%) to both parental clusters. Similar admixing has been reported for F1 or early-generation hybrids in other genera, such as *Helichrysum* (Galbany-Casals et al. 2012) and *Populus* (Deacon et al. 2017).

Further support of the hybridization event comes from the analysis of direct ITS sequences, as the hybrids exhibited an APS pattern indicative of the coexistence of divergent ribotypes inherited from the parental species. These additivities are a recognized hallmark of interspecific hybridization, particularly when concerted evolution has not yet homogenized

Table 3 Mean concentration (mg·kg⁻¹)±SD of total and phytoavailable elements in soils associated with *L. eschweii* (EST), *L. cossonianum* (MAC) and the hybrid (HYB)

	CTRL	EST	HYB	MAC
Total elements (mg·kg ⁻¹)	C	44,265.40±20,934.16	13,072.18±7944.92	18,158.00±15,864.95
	N	1219.58±277.55 ^a	808.12±82.10 ^{ab}	752.02±269.22 ^b
	P	473.00±67.90	509.17±68.30	482.45±91.46
	K	5398.82±703.05 ^{ab}	7510.59±324.44 ^c	6353.05±1526.02 ^{bc}
	Ca	45,680.41±26,432.63	21,622.18±20,757.87	19,236.09±23,464.55
Phytoavailable elements (mg·kg ⁻¹)	Mg	34,809.42±17,892.49	18,135.46±13,377.95	18,867.05±13,972.39
	S	482.58±162.63	559.52±185.76	560.14±385.44
	B	10.24±11.89	44.84±48.80	104.45±170.12
	Cu	19.83±5.16	22.36±7.77	23.68±6.35
	Fe	41,991.9±9714.05 ^b	51,762.58±5206.14 ^c	47,649.82±7812.06 ^{bc}
	Mn	857.33±122.53	666.71±242.81	674.15±176.08
	Mo	0.79±0.39 ^a	1.35±0.27 ^b	1.13±0.34 ^{ab}
	Na	1854.70±264.01	4121.66±504.86	3711.83±2175.56
	Sr	967.08±585.83	161.53±64.29	146.07±52.74
	Zn	204.52±21.56 ^b	82.09±8.27 ^a	128.39±59.71 ^a
	P	6.98±1.78 ^{ab}	8.74±5.18 ^b	6.22±2.28 ^{ab}
	K	43.05±7.11 ^a	109.73±35.10 ^b	116.74±44.50 ^b
	Ca	9406.19±3569.93 ^a	5224.41±1654.62 ^b	4695.86±1330.71 ^b
	Mg	3454.55±270.00 ^a	808.50±413.58 ^b	1750.84±986.83 ^{ab}
	S	84.82±28.77	224.42±104.96	380.44±309.70
B	8.99±0.75	15.05±7.11	9.20±6.42	
Cu	0.49±0.27	0.27±0.14	0.40±0.19	
Fe	12.41±2.26 ^a	6.58±0.75 ^c	9.34±0.54 ^b	
Mn	36.56±7.99 ^a	11.85±3.45 ^c	26.44±4.76 ^b	
Na	85.04±28.52 ^a	1813.80±791.01 ^b	1625.78±1469.02 ^{ab}	
Sr	190.54±8.58 ^a	60.34±48.01 ^b	81.87±55.54 ^{ab}	
Zn	0.92±0.31 ^a	0.00±0.00 ^b	0.01±0.02 ^b	

CTRL refers to soils collected outside the canopy of the studied species. Superscript letters indicate significant group differences based on the ANOVA ($p<0.05$). Only essential elements, Na and Sr are shown; for complete analyses see Tables S8 and S10

divergent nrDNA copies (Álvarez and Wendel 2003; Nieto-Feliner et al. 2004), and have been documented in various hybrid taxa (e.g., *Cirsium* × *vivantii*, Segarra-Moragues et al. 2007; *Convolvulus* × *despreauxii*, Carine et al. 2007; *Sidalcea virgata*, Whittall et al. 2000). Although alternative evolutionary mechanisms could produce similar outcomes (Aguilar et al. 1999; Salmerón-Sánchez et al. 2014), the fertile nature of the hybrids (Erben 1978) suggests that these additivities strongly reflect a recent hybrid origin.

Through cloning, we confirmed the presence of parental ribotypes, as well as additional polymorphic and potentially recombinant sequences within the genetic background of the hybrids. The arrangement of these clones in the phylogenetic network, with a wide range of variants frequently deviating from the parental clusters, likely reflects the presence of recombinant or chimeric ribotypes arising from recurrent hybridization among F1 individuals or unidirectional/bidirectional backcrossing events (Anderson and Hubricht 1938; Carine et al. 2007; Rieseberg 1997).

Backcrossing, also referred to as introgressive hybridization, poses particular conservation concerns in this context due to its potentially detrimental impact on *L. estevei*. Evidence from plant and animal systems shows that when a narrowly distributed endemic species coexists with a more widespread congener, gene flow can result in genetic assimilation and ultimately lead to the extinction of the endemic lineage (Levin et al. 1996; Rhymer and Simberloff 1996; Wolf et al. 2001). Nevertheless, the evidence gathered in this study points to asymmetric or unidirectional introgression occurring exclusively towards *L. cossonianum*, with no apparent signs of genetic erosion in *L. estevei*. This is supported by the coexistence of both exclusive ribotypes and ribotypes shared with the hybrid in *L. cossonianum*, and by the absence of recombinant ribotypes in the latter, where only pure (R2, R3 and R4) and polymorphic ribotypes congruent with its inherent genetic variability (R5 and R6) were identified (Table S4). The single polymorphic clone that did not follow the aforementioned trend (C6) could be better understood as a PCR-induced artifact rather than a genuine simple recombinant, given the lack of additivities at the corresponding locus (position 599) in any of the direct *L. estevei* sequences (Nieto-Feliner et al. 2004).

Asymmetric introgression is a relatively common phenomenon in nature (Arnold et al. 2010; Burgess et al. 2005; Marhold et al. 2002; Pimentel et al. 2010). For instance, Balao et al. (2015) described a hybrid zone similar to ours, in which unidirectional backcrossing affected only the widespread parental (*Onopordum nervosum*) while its rarer congener (*O. hinojense*) remained largely unaffected. In that system, strong postzygotic reproductive barriers were inferred as the most likely mechanism preventing backcrossing towards *O. hinojense*. In *L. estevei* the apparent genetic isolation may likewise result from robust reproductive barriers that remain uncharacterized. However, considering the relevance of preserving the genetic integrity of narrow endemics, further integrative research should be carried out to elucidate the mechanisms underlying this isolation. Such efforts would allow for the assessment of potential long-term risks of genetic swamping or demographic decline in populations of this species.

In addition, the presence of ribotypes typically associated with *L. estevei* in individuals morphologically and genetically identified as *L. cossonianum* may be indicative of incomplete lineage sorting (Comes and Abbott 2001; Pleines et al. 2009). An alternative hypothesis involves the action of biased concerted evolution toward the *L. estevei* ribotype, even though full convergence may not have been achieved due to the relatively limited evolutionary time elapsed (Nieto-Feliner and Rosselló 2007; Mitsui et al. 2011).

Table 4 Mean concentration (mg kg⁻¹) ± SD of mineral elements in foliar samples of *L. estevei* (EST), *L. cossonianum* (MAC) and the hybrid (HYB)

	EST	HYB	MAC
C	464,786.00 ± 9749.25 ^b	431,458.00 ± 14,104.32 ^a	424,406.00 ± 5687.10 ^a
N	12,953.00 ± 1562.58	11,965.28 ± 2356.50	13,823.20 ± 1498.99
P	420.20 ± 109.94 ^b	508.38 ± 195.46 ^b	730.24 ± 134.91 ^a
K	3864.28 ± 758.47 ^b	4174.63 ± 662.73 ^b	5852.36 ± 1173.75 ^a
Ca	3054.45 ± 1000.64 ^b	6154.01 ± 162.63 ^a	8264.99 ± 2920.63 ^a
Mg	4780.63 ± 1529.11 ^a	6970.46 ± 1071.84 ^b	5100.59 ± 1317.46 ^a
S	6997.03 ± 1766.56 ^b	11,931.02 ± 1366.81 ^c	16,070.88 ± 278.72 ^a
B	0.62 ± 1.12 ^b	1.06 ± 2.34 ^b	19.42 ± 7.68 ^a
Cu	3.69 ± 2.60	1.81 ± 0.58	2.86 ± 0.30
Fe	117.81 ± 47.13	91.02 ± 21.83	204.03 ± 138.81
Mn	44.82 ± 12.86 ^a	75.51 ± 19.82 ^b	49.90 ± 4.14 ^a
Mo	0.98 ± 0.45 ^b	0.72 ± 0.48 ^{ab}	0.25 ± 0.22 ^a
Na	6754.10 ± 775.82 ^b	4894.80 ± 1567.93 ^b	14,040.15 ± 2448.84 ^a
Sr	103.98 ± 9.67	195.48 ± 98.50	174.96 ± 45.10
Zn	7.00 ± 4.88 ^b	11.48 ± 7.31 ^{ab}	21.60 ± 10.00 ^a

Superscript letters indicate significant group differences based on the ANOVA ($p < 0.05$). Only essential elements, Na and Sr are shown; for the full analysis see Table S11

Morphometric analyses corroborated molecular results. Hybrids expressed a mosaic phenotype, with predominantly intermediate floral traits and leaf traits showing parental inheritance: overall morphology resembled *L. cossonianum*, whereas margin and phyllotaxis were typical of *L. estevei*. Among the characters assessed, 48% exhibited intermediate values between the parental taxa, suggesting that many morphological traits are influenced by co-dominant or quantitative inheritance. In contrast, 44% showed clear parental inheritance, reflecting a substantial retention of species-specific traits, as expected F₁ or early-generation hybrids, where additive and dominant genetic effects are prevalent (Rieseberg et al. 1993). Transgressive traits accounted for 8% of the total. These outlier traits are often the result of epistasis and may play a key role in fostering ecological divergence or the emergence of novel adaptations in hybrid lineages (Rieseberg et al. 1999). This trait distribution aligns with documented outcomes in other interspecific hybrids, as exemplified by the recently described *Carex × favratii* (Řepka and Mendel 2022).

Elementome as an innovative approach to analyze plant hybridization processes

Elementome analysis has gained relevance as a method to uncover ecological or biogeochemical niche divergence among closely related or co-occurring plant species (Pillon et al. 2018; Peñuelas et al. 2019). In this study, we expanded on traditional approaches, typically based on genetic and morphometric analyses, and occasionally on secondary metabolite profiling (Marhold et al. 2002; López-Caamal and Tovar-Sánchez 2014; Deacon et al. 2017), by integrating elemental profiling as an innovative and complementary tool to identify the hybridization event involving *L. cossonianum* and *L. estevei*.

Significant differences in soil pH and EC among soils associated with the three *Limonium* taxa highlight the existence of distinct edaphic niches. *L. estevei* prefers highly alkaline and conductive soils, consistent with its natural occurrence on rocky substrates featuring salt efflorescences. The elevated conductivity found beneath all taxa, relative to control soils,

suggests that these halophytes act as ecosystem engineers, modifying soil properties and Na levels (Wendelberger and Richards 2017).

The pronounced deficiency of N and P is typical of soils in southeastern Spain, where the arid climate promotes the presence of extensive gypsum outcrops and saline substrates (Merlo et al. 2011). Elementome profiling demonstrated that each taxon occupies a distinct biogeochemical niche. This finding was in line with Peñuelas et al. (2019), who argued that sympatric species tend to evolve divergent elemental compositions to mitigate competitive overlap. Interestingly, while PCA positioned the hybrid between parental taxa, ANOVA results revealed a mosaic pattern of elemental concentrations rather than a strictly intermediate profile. This pattern, reminiscent of observations in the morphometric analysis, suggests that hybrids may inherit functional traits in a non-additive manner, combining parental characteristics with potential transgressive features (Rieseberg et al. 1999).

To our best knowledge this is the first study to report a mosaic elementome in hybrid plants, supporting the use of elemental profiles to detect complex inheritance patterns beyond morphology and genetics. Such mosaicism, as noted by López-Caamal and Tovar-Sánchez (2014), may include intermediate, parental, or transgressive traits, affecting ecological interactions and stress tolerance. Future research should assess its prevalence across hybrids or in specific lineages like *Limonium*.

Following the discussion on elementome profiles, we examined the differential leaf concentrations of C, Na and K among the studied specimens (Table 4). The elevated C levels observed in *L. estevei* leaves can be associated with sclerophylly, a structural adaptation that enhances tolerance to arid, saline and nutrient-poor environments (Salleo and Nardini 2000). This trait may further reflect an extended lifespan, consistent with a resource-conservative strategy that relies on sustained, low-rate photosynthetic activity to optimize carbon assimilation over time in environments with limited resource availability (Wright et al. 2004).

We also observed differences in foliar concentrations of Na and K. In both cases, *L. cossonianum* exhibited higher levels compared to *L. estevei* and the hybrid individuals. While these disparities might initially be attributed to increased availability of these elements in soils inhabited by *L. cossonianum*, the analysis of total elements did not support this assumption. No significant differences were found in soil Na content between taxa, and K levels were actually lower in *L. cossonianum* soils (Table 3). According to Al Hassan et al. (2017), *Limonium* species with a narrow geographic distribution generally exhibit lower salinity tolerance thresholds. Adapted to edaphic environments with limited fluctuations, these taxa often rely on conservative strategies, limited to the compartmentalization or excretion of Na^+ and Cl^- ions into specialized foliar cells or organelles (Dassanayake and Larkin 2017; González-Orenga et al. 2021). In contrast, more broadly distributed species tend to display not only efficient Na^+ management but also active K^+ transporters, allowing for higher K^+ accumulation in leaves to maintain favorable Na^+/K^+ ratios, critical for enzymatic function and cellular homeostasis under salt stress (Al Hassan et al. 2017). The presence of such broader halotolerance mechanisms in *L. cossonianum* may therefore help explain the observed elemental differences. In addition, the hybrid's closer resemblance to *L. estevei* in Na management suggests inheritance of salt gland-mediated ion regulation and a more specialized tolerance strategy. Nonetheless, these hypotheses should be validated, as salinity tolerance in *Limonium* is highly species-specific and the cited literature focuses on related taxa rather than the species examined in this study.

Implications for the conservation of *L. estevei*

Until 2003, the only documented population of *L. estevei* comprised approximately 11,500 individuals, distributed across 20 demographically heterogeneous nuclei (Rodríguez-Tamayo et al. 2005a). Since then, a population decline exceeding 75% has been estimated, placing this already severely fragmented species in an extremely precarious conservation status (Gutiérrez et al. 2019). This critical situation is mainly driven by intense anthropogenic pressure on its narrowly restricted habitat, which represents its foremost threat. Urban expansion, driven by the considerable appeal of Macenas as a tourist destination, has led to the direct loss of approximately 3,700 individuals (Rodríguez-Tamayo et al. 2005b).

Specialized conservation sources, such as the *Red Book of Threatened Wild Flora of Andalusia* (Mota et al. 1999), identified hybridization with *L. cossonianum* as another major threat to the persistence of this endemic species. This concern stemmed from the possibility of imminent extinction of *L. estevei* as a pure ancestral lineage through genetic assimilation or “swamping”. However, our results demonstrate the absence of gene flow via introgression, contradicting these previously reported concerns.

Nevertheless, hybridization dynamics are stochastic, meaning that any perturbation in environmental conditions—whether natural or human promoted— could alter interactions between parental species, potentially shifting hybridization dynamics and even leading to the extinction of parental taxa (Bohling 2016). Therefore, despite the seemingly favourable genetic scenario, climate change and the anthropogenic pressure shouldn’t be overlooked, as they continue to pose significant risks to the long-term survival of *L. estevei* (Mota et al. 2004; Gutiérrez et al. 2019).

In this context, in situ and ex situ conservation strategies already implemented within the framework of the projects “*Actuaciones y Medidas de Conservación de Limonium estevei en el Plan Parcial ‘Macenas Playa Golf’ en Mojácar*” and LIFE Conhabit (Martín and Pérez 1992; Portal Ambiental de Andalucía 2025), should be complemented by additional measures, such as regular genetic monitoring and modelling of hybrid systems (Bohling 2016; Finger et al. 2024). Such approaches would allow the assessment of system dynamics over time and enable the early detection of potential introgression into *L. estevei*, providing managers with a wider range of management options than wouldn’t be available if introgression was already widespread before detection (Schwartz et al. 2007).

Leaving aside the genetic aspects, the limited success of translocation strategies implemented as compensatory measures to ensure the persistence of *L. estevei* individuals affected by the Mojácar urban development plan also warrants attention. Of the 3,000 affected individuals, 805 were relocated in 2003 to an experimental plot for post-relocation monitoring. After two years, only 154 remained, reflecting a survival rate of merely 19%. At present, only a few dozen persist. A comparable trend was observed for specimens transferred to El Albardinal Botanical Garden, where survival dropped to 33% barely one year after transplantation (Rodríguez-Tamayo et al. 2005b).

Based on our results, this low persistence is primarily attributable to the species’ strict biogeochemical niche requirements. These data indicate that any reduction in its area of occupancy is likely to result in an irreversible loss of individuals. Accordingly, conservation strategies should prioritize the preservation and active management of natural habitats, rather than relying solely on mitigation actions with low success, such as those implemented to date.

Concluding remarks

The occurrence of a backcrossing event between hybrid forms and *L. cossonianum* was confirmed. No evidence of backcrossing with *L. estevei* was found. This result has significant implications for conservation, as the absence of introgression into *L. estevei* suggests there is no immediate risk of genetic deterioration or “genetic swamping” to its only known population, quite contrary of what was previously suspected.

Despite the great morphological similarity among species in the genus *Limonium*, the differences observed in the vegetative and reproductive traits between *L. cossonianum* and *L. estevei* facilitated the identification of individuals with intermediate morphological features. These observable patterns provided a solid basis for subsequent genetic analyses. Hybrid individuals resulting from the cross between *L. cossonianum* and *L. estevei* were originally reported by Erben (1978). Based on the robustness and consistency of our evidence, we formally propose the recognition of this taxon as a nothospecies. A complete taxonomic treatment, including diagnosis, detailed morphological description, etymology, and distribution, is currently in preparation (Miranda-Hernández et al. in prep.).

This research reveals a clear edaphic niche differentiation between the species, with pH and EC emerging as key factors. *L. estevei* is associated with the least abundant soils in the area, which are also the most distinct from both control soils and those of *L. cossonianum*. This marked edaphic specificity explains the limited success of translocation efforts undertaken as compensatory measurements to mitigate anthropogenic impacts. Therefore, any reduction in its area of occupation is an irreversible loss of individuals, underscoring the preservation of its highly specialized habitat as the only realistic conservation strategy. By contrast, *L. cossonianum* grows in soils more similar to those widespread in the area, suggesting a lower edaphic specialization. The hybrid, in turn, occupies soils comparable to those of *L. estevei*.

In terms of foliar elemental composition, *L. estevei* and the hybrids show comparatively fewer differences in their profiles, a pattern that could suggest potential competition between the endemic species and the hybrid. However, this does not appear to be the case, as each taxon occupies a distinct and non-overlapping biogeochemical niche.

Finally, this research documents for the first time a “mosaic pattern” in the elementome of hybrid plants, suggesting they inherit functional traits in a non-additive manner. This finding demonstrates the potential of elemental profiling as an innovative tool for detecting complex inheritance patterns. When integrated with traditional morphological and genetic analyses, this approach could provide a powerful framework for assessing the extent to which hybridization threatens the preservation of other endangered flora beyond the specific case examined here.

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Data Availability Data is provided within the manuscript or supplementary information files.

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