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RESEARCH

# Population genetic structure and patterns of hybridization of the rare *Lupinus tidestromii* and its congener *L. chamissonis* (Fabaceae) inform seed sourcing strategies for population augmentation and reintroduction

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**Abstract**
Human activities can impact the genetic diversity of populations, making them more vulnerable to extinction. Rare species are at an increased risk of negative genetic consequences of human activities, but understanding genetic diversity in rare species requires comparison to more common congeners. Hybridization, a common phenomenon in plants, can provide genetic rescue of genetically depauperate populations or put rare species at risk of being "swamped" out of the population. Human-mediated dispersal can create novel sympatry between previously allopatric species, fostering hybridization. The endangered Tideström's lupine (*Lupinus tidestromii* Greene), endemic to the coastal dune ecosystem of California, co-occurs and hybridizes with the more common dune bush lupine (*L. chamissonis* Eschsch.). We characterized 532 individuals from sympatric and non-sympatric sites across both species' entire geographic ranges using genotyping-by-sequencing technology to identify 1,377 single-nucleotide polymorphisms. We analyzed population structure, genetic diversity within and among populations, and hybridization between *L. tidestromii* and *L. chamissonis*. Genetic diversity was lower in *L. tidestromii* than in the more common *L. chamissonis*. Both species showed strong population structure which coincided with a deep intraspecific split between populations north and south of San Francisco. Hybridization was confirmed at all sites of co-occurrence. Evidence of hybridization at multiple non-sympatric sites indicated former co-occurrence and recent local extirpations. From these results, we make specific management recommendations for *L. tidestromii*. Seeds from large populations in the north can be used to augment the smaller populations in this region and to reintroduce this endangered species back to extirpated sites. Our results highlight how studies considering spatial patterns of genetic diversity, hybridization and private alleles can be used to make clear recommendations for conservation actions.

**Keywords** Genetic structure · Hybridization · ddRAD · Single nucleotide polymorphisms · *Lupinus* · Coastal dunes

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## Introduction

Human activities, such as the introduction of exotic species, land use change, and climate change, are threatening approximately 25% of all species, with the current extinction rate estimated to be tens to hundreds of times higher than the background rate of extinction (IPBES et al. 2019; Ceballos et al. 2015). Anthropogenic activities can also impact biodiversity at the genetic level, one of the three primary targets of biodiversity conservation within the framework of the Convention of Biological Diversity (Secretariat of the Convention of Biological Diversity 2020). Human modification of habitats can cause bottleneck

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events, increase genetic drift, increase inbreeding, and decrease gene flow between populations for the species that occupy modified habitats (Young et al. 1996; Allendorf et al. 2001; Carvalho et al. 2019). These processes result in reduced genetic diversity, especially for rare species and taxa with small populations (Ellstrand and Elam 1993; Cole 2003). Reductions in genetic diversity may result in reduced reproductive fitness and the decreased ability of a population to adapt to changes in environmental conditions or recover from extreme anomalies (Reed and Frankham 2003; Reusch et al. 2005; Willi et al. 2006). On the other hand, human action may initiate hybridization of previously isolated species, thus leading to gene flow between species and potentially threatening rare species (Allendorf et al. 2001).

Rarity results through the combined effects of multiple processes such as geographic range size, habitat specificity, and local population size (Rabinowitz 1981). Broadly, theory predicts that rare species should have lower diversity than more common species, due to greater genetic drift in small populations (Wright 1931) and directional selection to occupy specialized habitats (Van Valen 1965). However, rarity as defined by Rabinowitz (1981) also includes species that are geographically restricted but locally abundant and therefore have higher genetic diversity than expected (e.g. Harrison et al. 2019; Young and Brown 1996). Meta-analyses that compare the genetic diversity of rare and common species consider phylogenetic history to disentangle the biogeographic effects resulting in rarity from phylogenetically-conserved traits that also influence genetic diversity, such as breeding system and life form. The results of these studies support the prediction that rare species have relatively lower genetic diversity than their common relatives (Gitzendanner and Soltis 2000; Boyd et al. 2022). In the context of conservation, comparing a rare species and its more widespread congener is useful as the widespread congener provides context that can be used to define "low" genetic diversity (Gitzendanner and Soltis 2000).

Hybridization is a common phenomenon in plants which serves as an evolutionary force driving adaptive evolution and speciation (Anderson 1953; Ellstrand et al. 1996; Rieseberg and Carney 1998; Rieseberg et al. 2003; Martin et al. 2006). Hybridization occurs between closely related species that have the ability to reproduce, which in plants is mediated by processes such as shared pollinators, pollen compatibility, overlapping phenology, and the production of fertile hybrid offspring (Ellstrand et al. 1999). For the conservation of rare species, hybridization has been discussed both as an extinction threat and as a process that can facilitate species recovery (Chan et al. 2019; Draper et al. 2021). Hybridization can act as a threat to populations and species through asymmetric introgression, defined as uneven gene flow caused by unidirectional backcrossing of hybrids to the more abundant parent lineage (Levin et al. 1996; Rhymer and Simberloff 1996; Buerkle et al. 2003). Hybridization is typically viewed negatively when human activities, such as species introductions, cause previously isolated taxa to come in contact, introducing novel hybridization events (Allendorf et al. 2001; Mooney and Cleland 2001; Abbott et al. 2003). However, in other situations, hybridization has been viewed as a positive process for conservation that can provide evolutionary rescue of rare species and reservoirs of genetic diversity (Chan et al. 2019; Brauer et al. 2023). For species of conservation concern, especially those which hybridize with a more common congener, evaluating the frequency and consequences of hybridization is essential to informing management decisions (Glennon et al. 2011).

Sourcing seed for reintroductions and rescue of declining populations is an important question in conservation genetics. On one hand, sourcing seed from nearby sites may preserve the genetic integrity of the species and these seeds might have higher fitness due to local adaptation (Bucharova et al. 2019). On the other hand, supplementing seed from more distant populations can boost local genetic diversity and may increase plant fitness and adaptive potential (Broadhurst et al. 2008; Aitken and Whitlock 2013; Bürli et al. 2024). Hybridization adds a layer of complexity to seed sourcing, as the translocation of individuals to a recipient population can result in novel hybridization events (Weeks et al. 2011). Understanding the population genetics of the source and recipient populations, including the genetic divergence between the populations and presence of hybrid individuals, is critical to making informed conservation decisions about seed sourcing for reintroductions and rescue of declining populations (Weeks et al. 2011; Frankham et al. 2011; Hoffmann et al. 2021).

*Lupinus tidestromii* Greene is an endangered perennial plant species endemic to coastal California facing numerous threats including habitat loss, invasive species, and climate change (USFWS 1998; Pardini et al. 2017; Pardini et al. 2018; Compagnoni et al. 2021). *L. tidestromii* co-occurs and is known to hybridize with its more common congener, *L. chamissonis* Eschsch. Ten of the 18 extant populations of *L. tidestromii* occur at Point Reyes National Seashore (PRNS). Long-term monitoring indicates that viability of the three southern PRNS populations is threatened due to steadily dwindling plant numbers, despite adaptive management and habitat restoration, whereas the Abbotts Lagoon population located in northern PRNS is thriving in response to these actions (Pardini et al. 2018; Compagnoni et al. 2021; Parsons

2022). Genetic issues may play a role in the decreased fitness of the southern populations, and conservation actions involving collecting seeds from northern populations to augment population size and genetic diversity of southern populations are being considered. To best inform management decisions for *L. tidestromii* at PRNS and elsewhere, the within and among population genetic variation of *L. tidestromii*, *L. chamissonis*, and their hybrids across their entire respective ranges were analyzed, including sites of sympatry and non-sympatry. This study aimed to characterize the geographic patterns of genetic diversity in these species, to compare the rare *L. tidestromii* with the more common *L. chamissonis*, and to identify any potential deleterious genetic processes in the endangered *L. tidestromii*. Additionally, to better understand the dynamics of hybridization, the population genetics analyses were used to identify sites of modern and historical hybridization. The results inform management recommendations for seed sourcing and movement for the endangered *L. tidestromii*.

## Materials and methods

### Study species

*Lupinus tidestromii* Greene and *L. chamissonis* Eschsch. (Fabaceae) are two perennial herb species endemic to California occurring on coastal sand dunes. *L. tidestromii* is limited to two disjunct clusters of populations (north of San Francisco and on the Monterey Peninsula) that are considered distinct varieties (Fig. 1; USFWS 1998; Eastwood 1938; Howell 1986; Riggins and Sholars 1993). The vast majority of all *L. tidestromii* individuals occur at Point Reyes National Seashore (PRNS; USFWS 1998). *Lupinus chamissonis* is more widespread, occurring as far north as Sonoma County and as far south as Los Angeles County (Sholars and Riggins 2022). The two species are known to hybridize due to their shared pollinators (*Bombus* sp.) and overlapping flowering periods (T. Moss, personal communication 2024; E. Pardini, personal observation). While *L. tidestromii* and *L. chamissonis* occupy different

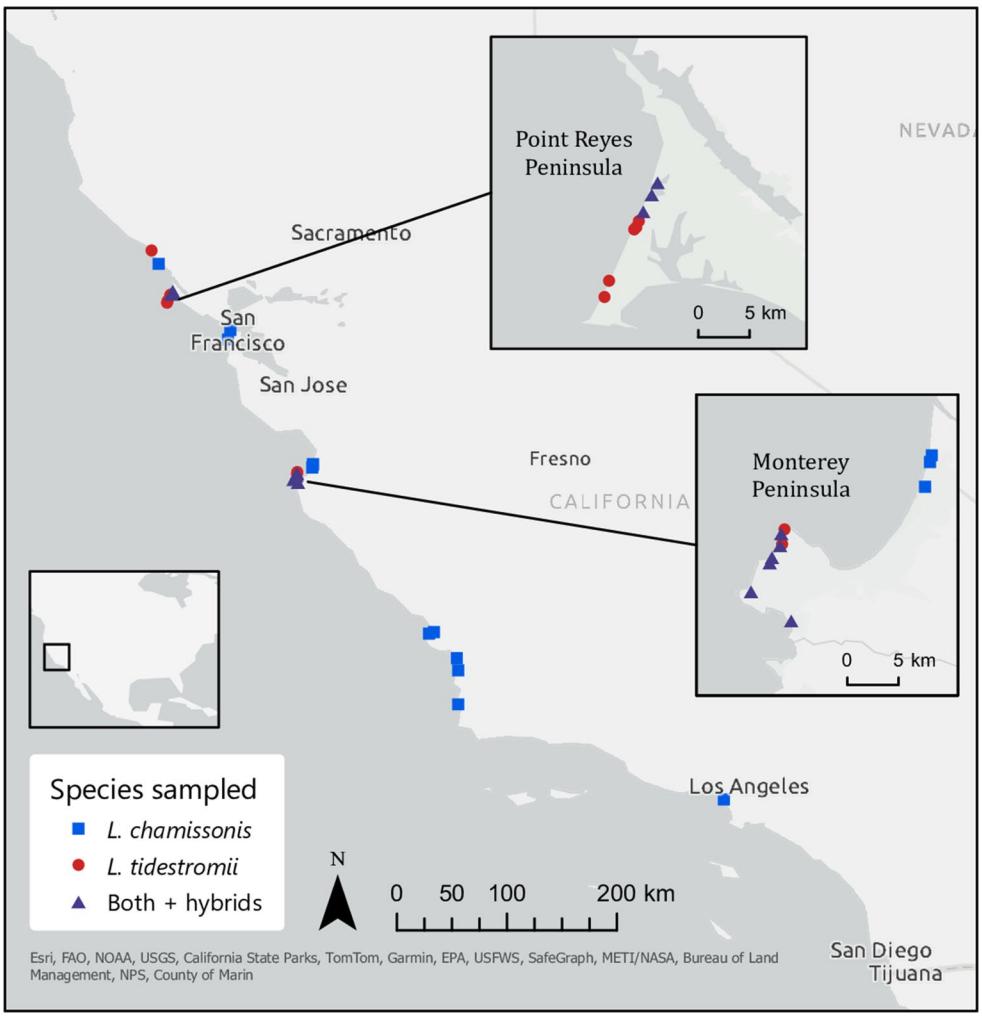


**Fig. 1** Map of sampled populations of *Lupinus tidestromii* and *L. chamissonis* in the state of California, USA. Species sampled at each site is indicated by point color and shape. More details of sampling sites provided in Table 1. Inset maps to the right show the details of the two main sampling areas, Point Reyes National Seashore (PRNS) on the Point Reyes Peninsula and the Monterey Peninsula (MON)

types of dune habitats – early to mid-successional dune mat and late-successional dune scrub, respectively – these habitats often adjoin each other due to topographic heterogeneity, enabling gene flow exchange between these species. At the PRNS populations, the co-occurrence is natural, whereas in the Monterey area, *L. chamissonis* was introduced starting in the 1960's as a horticultural plant. Unlike most perennial lupines, *L. tidestromii* is self-compatible (Juncosa and Webster 1989; Coppoletta 2005); self-compatibility in *L. chamissonis* has not been investigated. Dispersal capabilities of both species are limited. Seeds disperse by explosive dehiscence and are usually found within a meter of the parent plant in *L. tidestromii* (USFWS 1998; Parsons 2022).

## Sampling

Sampling locations were chosen to represent the complete geographic ranges of both species, which divide into three regions: Northern California, Monterey, and Southern California (Table 1). Nearly all known occurrences of *L. tidestromii* were sampled. A total of 29 sites were sampled: 8 sites where only *L. tidestromii* was expected to occur, 12 sites where only *L. chamissonis* was expected to occur, and 9 sites of expected sympatry (Fig. 1). Sites were characterized as dune mat or dune scrub communities with climate classed as Köppen class Csb, characterized by a mild Mediterranean climate with wet winters and dry summers (Kottek et al. 2006; Beck et al. 2018). Sites were sampled between 8 March and 20 June 2023, with the exception of

**Table 1** Overview of sampling sites. At sites where both species were expected to occur, population size and area refers to all focal lupines with no distinction made between the studied taxa

| Site name | Abbreviation | Location | Population size | Area (hectares) | Species expected |
|---|---|---|---|---|---|
| Northern California | *N* | 37.7° − 38.5° *N* | | | |
| Goat Rock | GR | Sonoma Co. | 500 | 0.8 | LT |
| Bodega Bay | BBY | Sonoma Co. | 500 | 0.2 | LC |
| Abbotts Lagoon North | AbbN | PRNS | 300 | 0.4 | LT, LC, HY |
| Abbotts Lagoon | Abb1 | PRNS | 400,000 + | 20 + | LT, LC, HY |
| ATT | ATT | PRNS | 2,000 | 1.1 | LT, LC, HY[†] |
| Population 9 | Pop9 | PRNS | 1,100 | 0.4 | LT |
| North Beach | NB | PRNS | 90 | 0.4 | LT |
| North Beach - Bathroom | NBB | PRNS | 1,200 | 0.6 | LT |
| Davis | Davis | PRNS | 200 | 0.7 | LT |
| B Ranch North | BRN | PRNS | 1,100 | 3.2 | LT |
| Baker Beach | BKB | San Francisco Co. | 150 | 6.1 | LC |
| Fort Funston | FFN | San Francisco Co. | 150 | | LC |
| Monterey | MON | 36.5° − 36.8° N | | | |
| Marina Dunes Sanctuary Resort | MSR | Monterey Bay | 75 | 0.8 | LC |
| Marina SB | MAR | Monterey Bay | 25 | 0.8 | LC |
| Fort Ord Dunes SP | FOD | Monterey Bay | 190 | | LC |
| Pacific Grove - Links | PGR | Monterey Peninsula | 100 | 0.3 | LT[a] |
| Great Tide Pool | GTP | Monterey Peninsula | 300 | 0.7 | LT, LC, HY[a] |
| Pico Ave Private Property | PAV | Monterey Peninsula | 250 | 0.4 | LT |
| Asilomar SB | ASB | Monterey Peninsula | 200 | 0.5 | LT, LC, HY[a] |
| Spanish Bay | SBY | Monterey Peninsula | 350 | 0.1 | LT |
| Spanish Bay Road | SBR | Monterey Peninsula | 200 | 0.2 | LT, LC, HY[a] |
| Signal Hill | SHL | Monterey Peninsula | 450 | 0.8 | LT, LC, HY[a] |
| North Dunes at Carmel Beach | CD | Monterey Peninsula | 700 | 0.4 | LT, LC, HY[a] |
| Southern California | S | 33.9° − 35.4° N | | | |
| Morro Bay SP | MB | San Luis Obispo Co. | 30 | 1.4 | LC |
| Montaña de Oro SP | MDO | San Luis Obispo Co. | 35 | 1.3 | LC |
| Pismo Dunes | PD | San Luis Obispo Co. | 500 | 4 | LC |
| Oceano Dunes SVRA | OD | San Luis Obispo Co. | 1,000 | 40 + | LC |
| Vandenberg Space Force Base | VSFB | Santa Barbara Co. | 65 | 0.6 | LC |
| Ballona Wetlands | BW | Los Angeles Co. | 110 | 4.8 | LC |

[a] Sites where supplementary sampling took place in June 2023 to ensure the sampling of hybrid individuals

*LTLupinus tidestromii*, *LCLupinus chamissonis*, *HY* hybrids of *L. tidestromii* and *L. chamissonis*, *PRNS* Point Reyes National Seashore, *SB* State Beach, *SP* State Park, *SVRA* State Vehicle Recreation Area

most sites at PRNS which were sampled in late June to early July 2021.

At each site, samplers recorded information about the population, including GPS coordinates of the center of the population, an estimate of the total number of individuals present, and an estimate of the area occupied by the target species. At sites where both species occurred, the population information was recorded for the entire collective population of both species and their hybrids, without unique distinctions for each species.

Sites varied greatly in the number of individuals present (25 to 400,000 + individuals) and area (0.1 to 40 + hectares) (Table 1). Thus, the sampling protocol varied slightly between sites. In general, 12–20 individuals were sampled along a transect crossing the population at its widest point. In large, dense populations, individuals were sampled at a fixed distance along the transect, one individual selected every five meters until 20 individuals were sampled. In sparse populations, every individual on the transect was sampled until 20 individuals were sampled. If fewer than 20 individuals occurred on the transect, a second transect at least five meters apart from and parallel to the first was sampled. In very small populations, all individuals were sampled. At the largest population (Abb1), individuals were selected along a wandering transect which covered the majority of the native dune habitat. Samplers at Abb1 targeted individuals which appeared to be pure *L. tidestromii* and individuals which appeared morphologically intermediate between *L. tidestromii* and *L. chamissonis*. At some sympatric sites, an additional individual selection occurred to ensure sufficient sampling of potential hybrid individuals (Table 1). After sampling along the transect at these sites, samplers haphazardly selected additional individuals at least 5 m from the transect to ensure a minimum of 12 individuals of each species plus up to 12 putative hybrids were sampled at the site, when possible. Thus, the numbers of pure species and hybrids sampled per population does not necessarily reflect their true proportions.

Differentiating between *L. tidestromii*, *L. chamissonis*, and hybrids thereof at sites of co-occurrence was based on Yadon (2003). In general, *L. tidestromii* is a prostrate herb, with 3–5 leaflets per leaf which exhibit long, shaggy leaf hairs. Each inflorescence has 2–3 whorls of flowers. This species features a prominent yellow spot on the flower banner and a yellow-green calyx. Wooly hairs are present on the margin of the keel. Conversely, *L. chamissonis* is an erect shrub, with 5–9 leaflets per leaf which exhibit short, appressed leaf hairs. Each inflorescence has 4–8 or more whorls of flowers. This species generally lacks the yellow spot on the flower banner and has a grey-violet calyx. Flower color can be much more variable than in *L. tidestromii*, ranging from white to deep violet. Keel hairs are absent. Hybrid morphology varies greatly and hybrids often present with a mix of characters from both species, or variously intermediate characters.

Adult individuals were selected for sampling when possible. At each selected individual, 3–5 undamaged, healthy leaves were collected for molecular analysis. The leaves were dried and stored with silica gel before processing. Leaves from a total of 551 individuals were processed for analyses. The GPS coordinates of each individual were also recorded at the time of sampling.

## Molecular analysis

DNA was extracted using DNeasy 96 extraction kits (QIAGEN). ddRAD libraries were generated for a total of 551 individuals following the protocol of Peterson et al. (2012) using 100 ng DNA per sample, EcoRI and MseI as restriction enzymes and one of 96 7 bp barcodes and one of 12 5 bp indices; for details of the lab procedure see Durka et al. 2024. Dual-index libraries were sequenced (PE150) on Novaseq 6000 sequencing systems resulting in a total of 476.3 Gb of sequence data, i.e. on average 2.94 Mio concatenated sequences per individual. After demultiplexing, sequences were used to identify and genotype single nucleotide polymorphism (SNP) markers using the dDocent pipeline (Puritz et al. 2014) which then underwent subsequent SNP filtering (O'Leary et al. 2018). Filtering retained biallelic SNPs with a minimum read depth of 3, excluded markers showing fixed heterozygosity and skipped individuals with >75% missing data, followed by filtering SNPs for allele balance, missingness (<66%), minor allele frequency (0.05) and minimum (10) and maximum (1000) mean read depth, finally retaining only one marker per contig. For details on parameters used in the bioinformatic analyses, see Durka et al. 2024. The final data set consisted of 532 samples and 1,377 biallelic SNP markers with 10.94% missing data. Species specific data sets were again filtered for minor allele frequency (0.05) and comprised 1,179 and 1,359 SNP markers in *L. tidestromii* and *L. chamissonis*, respectively.

Raw sequence data is available from the European Nucleotide Archive (https://www.ebi.ac.uk/ena) under acce ssion number PRJEB72106 and individual sample numbers ERS17855825 - ERS17856375.

## Population genetics analysis

### Identification of species and hybrids

Species and hybrid identities of all individuals were assigned using NewHybrids v.1.1 (Anderson and Thompson 2002) with implementation in R via dartR v.2.9.7 (Gruber et al. 2018; Mijangos et al. 2022). Due to the limitations of

NewHybrids, 200 loci were selected for input using the AvgPIC method described in the GL.NHYBRIDS function. The program ran for 10,000 MCMC iterations with 1000 iterations as the burn-in and a threshold of 0.05. Taxon identities were determined based on the posterior probabilities of an individual's assignment to the different hybrid classes, i.e., pure parental 0 (P0, *L. tidestromii*), pure parental 1 (P1, *L. chamissonis*), $F_1$ hybrid ($F_1$), $F_2$ hybrid ($F_2$), backcross to P0 ($F_1$xLT) or backcross to P1 ($F_1$xLC). Individuals were assigned to the class which corresponded to a greater than or equal to 90% posterior probability of assignment. When an individual did not have at least a 90% posterior probability of belonging to a single class, assignments were made on a case-by-case basis and were assigned to the most likely class (5 individuals, highest posterior probabilities between 54% and 85%). Taxon identities from the NewHybrids analysis were used for all subsequent genetics analyses, as either the direct output (6 classes: LT, LC, $F_1$, $F_2$, $F_1$xLT, $F_1$xLC) or modified to group all hybrid individuals together (3 taxa: LT, LC, HY).

### Population structure

Genetic relationships among samples were displayed with principal components analysis (PCA) of the SNP dataset implemented in R via ADEGENET v.2.1.10 (Jombart 2008; Jombart and Ahmed 2011). A PCA of all individuals was followed by subsetted PCAs of each pure species (LT and LC from NewHybrids).

**ADMIXTURE analysis** For a model-based approach to population assignment, ADMIXTURE v. 1.3.0 (Alexander et al. 2009; Alexander and Lange 2011) analysis was performed on the complete dataset. The analysis was run for values of *K* ranging from 2 to 22 resulting in individual ancestry coefficients for each of the respective number of gene pools. The statistically preferred value of *K* was chosen as that with the lowest cross-validation error. Additional analyses were run on datasets of each pure species. We refer to the ADMIXTURE clusters at the statistically preferred value of *K* as natural populations after cross checking between total and single species analyses and PCAs.

**Chloroplast haplotype analysis** We aimed to categorize which SNP loci originated from the maternally inherited chloroplast genome, as this potentially enables us to trace maternal lineages and thereby explore the dynamics of hybridization, including the directionality of crosses and potential asymmetries in introgression.

Because no complete plastome sequence exists for our study species, we used the dDocent reference sequences as query sequence set and searched for homologous plastid regions by performing a BLASTn search against the NCBI nt database (2025-03-31). To ensure taxonomic relevance, we restricted hits to *Lupinus* (entrez_query: "Lupinus[Organism]") and applied an e-value threshold of $10^{-12}$.

When the field "salltitles" of the results contained one of the keywords "plastid" or "chloroplast", query sequences were considered putatively chloroplast. A total of 33 SNPs (2.4%) were thus identified as putative cpDNA-SNPs. A reduced dataset containing only the 33 putative cpDNA-SNPs was generated which first underwent PCA analysis. We used k-means clustering to identify the likely number of groups using the FIND.CLUSTERS function from ADEGENET and the BIC statistic and assigned individuals to the respective cpDNA groups. For individuals with missing data or heterozygous genotypes at the decisive locus C_1640, the cp. group was set missing (NA). For further details on the analysis of cpDNA SNP loci, see Supplementary Text S1.

### Genetic diversity

Genetic diversity was first examined at the species level as overall expected ($H_E$) and observed heterozygosities ($H_O$). The same heterozygosities plus inbreeding coefficients ($F_{IS}$) were also calculated within each site using the GL.REPORT.HETEROZYGOSITY function in the R package DARTR v.2.9.7 (Gruber et al. 2018; Mijangos et al. 2022). To calculate these descriptors at the natural population level, weighted means of each descriptor were calculated from the site-level values of the sites contained within each natural population. The number of private alleles at levels of species, natural population and site were performed using the function GL.REPORT.PA in DARTR, excluding hybrid individuals. Analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed on different sets of samples to quantify genetic differentiation among taxa, regions, natural populations and sites using the POPPR.AMOVA function in the R package POPPR v.2.9.4 (Kamvar et al. 2014, 2015) with PEGAS implementation and 200 permutations. To examine genetic differentiation between sites, pairwise $F_{ST}$ values were calculated for each site pair using STAMPP v.1.6.3 (Pembleton et al. 2013), examining each pure species independently and excluding hybrids. Overall $F_{ST}$ values were also calculated at the species level, and at the regional level within each species. Isolation-by-distance was investigated using a Mantel test for a relationship between the standardized $F_{ST}$ values ($F_{ST}$ / (1 - $F_{ST}$)) and $\log_{10}$-transformed pairwise geographic distances between sites with VEGAN v.2.6-4 (Legendre and Legendre 2012; Oksanen et al. 2022). For *L. tidestromii* linear regressions were performed with population size as the predictor and $H_O$ and $F_{IS}$ as the response

variables to examine the relationships between population size and genetic diversity.

### Hybridization

At each sampling site, the taxon composition of the sampled individuals from the NewHybrids analysis was compared to modern expected occurrences and historical records. Modern expected community composition and historical records were derived from personal observation by the authors spanning from 2008 to 2023, consultation with local land managers and botanists, observations posted on iNaturalist, and range maps and herbarium specimens cataloged on CalFlora (2023; J. Dorrell-Canepa, T. Moss, P. Regan, personal communications 2024).

Sampled individuals were then pooled across natural populations which occurred at the same geographic locations to determine which natural populations of *L. tidestromii* hybridized with those of *L. chamissonis*.

## Results

### Population genetics

#### Identification of species and hybrids

NewHybrids analysis generated assignments to a hybrid class for 527 out of 532 individuals with >90% posterior probability (Figure S1). Five individuals with lower posterior probabilities were assigned to the class exhibiting the highest probability. Overall, 215 individuals were assigned to *L. tidestromii* (LT), 203 were assigned to *L. chamissonis* (LC), 32 and 11 were assigned to hybrid classes $F_1$, $F_2$, and 36 and 35 to backcrosses $F_1$xLT and $F_1$xLC, respectively. For further analyses, hybrid classes $F_1$, $F_2$, and backcrosses were collected into a single category of hybrids (HY, $N=114$).

#### Population structure

The PCA analyses showed strong genetic differentiation within, and hybridization between, species. PCA of all samples revealed a clear separation between *L. tidestromii* and *L. chamissonis* along the first PC (47.1% variation explained), with hybrids at intermediate positions, reflecting the taxon assignments of NewHybrids. Segregation of individuals along the second PC (10.7% variation explained) corresponded to a latitudinal separation between two regions (N vs. MON+S; Fig. 2) in both species. PCA of only *L. tidestromii* revealed strong hierarchical differentiation and distinguished two major geographic groups, each exhibiting substructure (Fig. 3b, c). The two groups segregated along PC1 (65.2% variation explained) corresponded to sites at Monterey and sites in Northern California. Along PC2 (2.97% variation explained), the sites at Monterey were further segregated into two groups. Along PC3 (1.7% variation explained), the two southern populations at PRNS were separated from the rest of the sites in Northern California (Fig. 3c). PCA of only *L. chamissonis* revealed strong hierarchical differentiation and first distinguished three major groups along PC1 and PC2 (Fig. 3e, f) corresponding to the three geographic regions. The group to the south of Monterey was further structured into three groups by PC3 and PC4 (BW, VSFB+OD+PD, MDO+MB; Fig. 3b, c).

**ADMIXTURE analysis** Model based cluster analysis using all SNP markers with ADMIXTURE confirmed the hierarchical

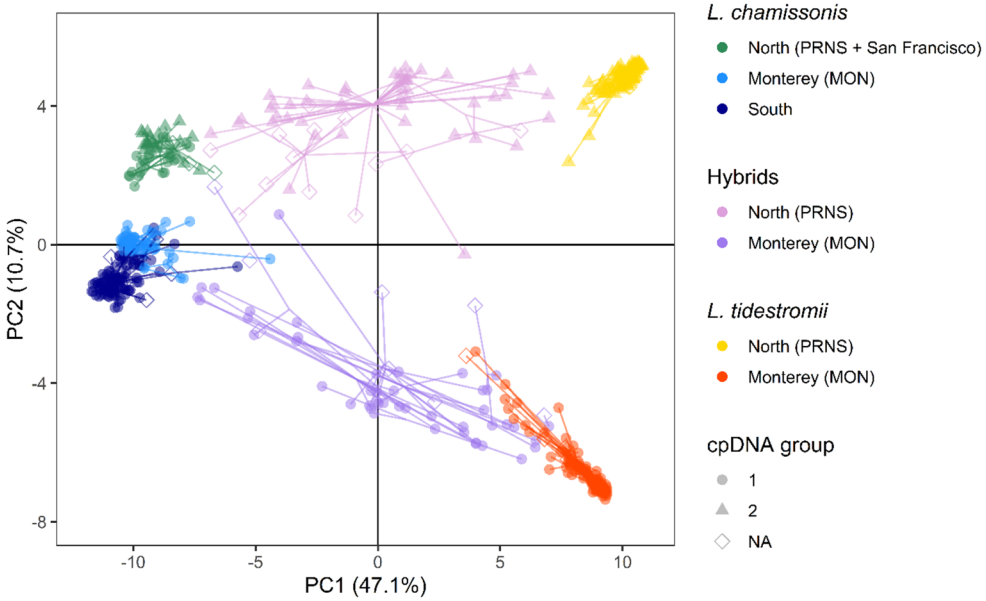


**Fig. 2** Principal components analysis of 532 *Lupinus* individuals based on 1,377 biallelic SNP markers. Individuals are colored according to species designations from NewHybrids and the natural population they belong to. Point shapes correspond to cpDNA groups. Lines connect individuals belonging to the same natural populations

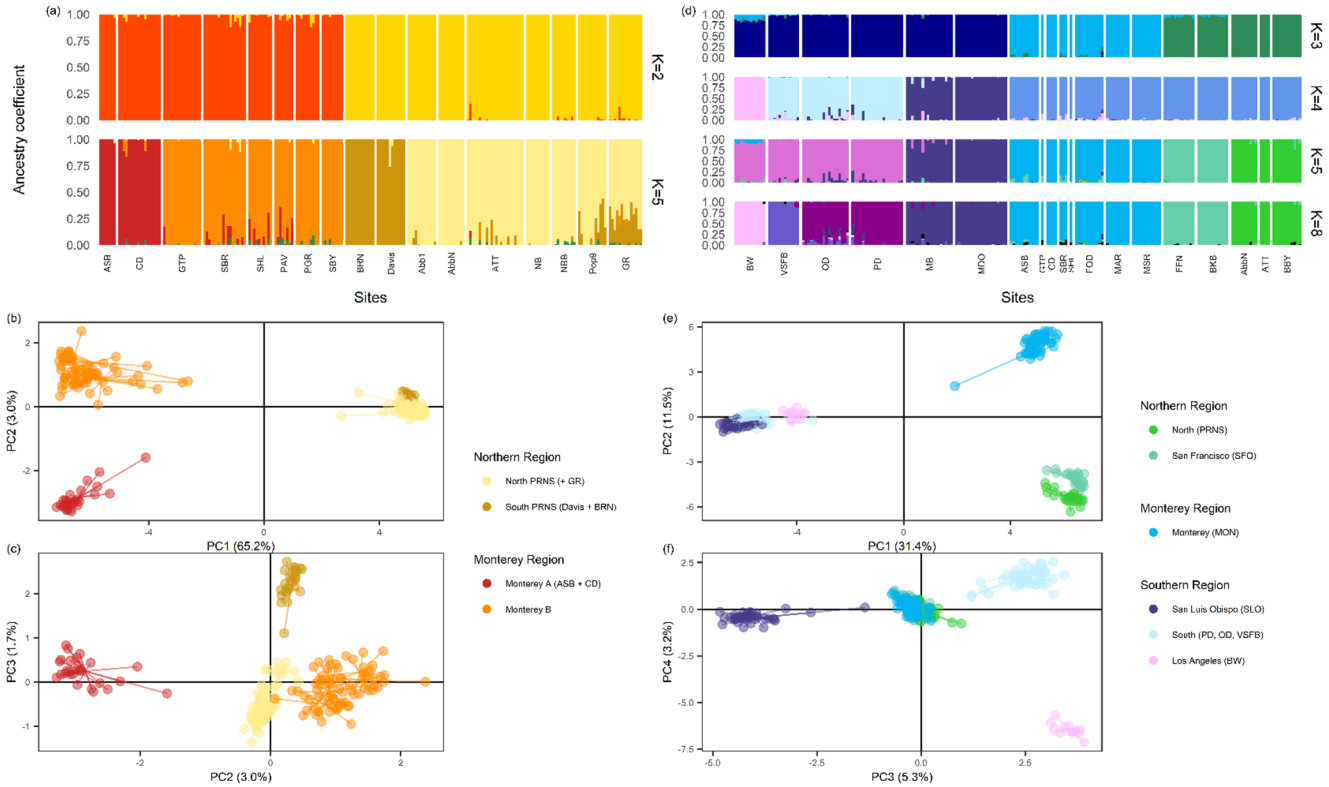


**Fig. 3** Population structure of 218 pure *L.tidestromii* (**a**-**c**) and 204 *L.chamissonis* (**d**-**f**) individuals. **a** Population structure and individual admixture for *L. tidestromiiK* =2 and *K* = 5, and (**d**) for *L.chamissonisK* = 3 through *K* = 5, and *K* = 8. For both ADMIXTURE plots, each individual is represented by a column that is partitioned into sections that depict the individual's coefficient of ancestry into each of the *K* clusters. Individuals are grouped according to the site they were sampled from. Sites are ordered from south to north along the x axis. **b**, **c** Principal components analysis of 218 *L. tidestromii* individuals based on 1,093 SNP markers, showing PC1 and PC2 (**b**) and PC2 and PC3 (**c**). Individuals are colored according to the natural population they belong to. **e**, **f** Principal components analysis of 204 *L. chamissonis* individuals based on 1,377 SNP markers, showing PC1 and PC2 (**e**) and PC3 and PC4 (**f**)

structure detected in the PCA. For L. tidestromii and excluding hybrids, the cross-validation error indicated K = 2 major groups with further fine structure up to K = 5 groups (Figure S2a). At K = 2, the clusters represented a primary distinction between the Northern California and Monterey regions, while at K = 5 in both these regions two clusters emerged representing geographic population groups (Fig. 3a). One cluster at K = 5 (green) occurred only as a minor admixture proportion in a minority of individuals without geographic focus. This minor group was also present at K = 3 and K = 4 where it obscured the within-region substructure.

For L. chamissonis and excluding hybrids, the cross-validation error indicated that there were K = 8 hierarchically structured clusters (Figure S2b). At K = 3, the three clusters represented the three sampled regions (Fig. 3d). At K = 4, Monterey and Northern California were clustered together, and Southern California was represented by three clusters which corresponded to the geographic population groups seen in the PCA (Fig. 3f). At K = 5, two clusters represented the northern and southern populations in Southern California, respectively, one cluster represented the Monterey region, and two clusters represented San Francisco and north of San Francisco in Northern California. At K = 8, the southernmost cluster in Southern California seen at K = 5 was further subdivided into three clusters.

When all samples were analyzed, i.e., both species plus hybrids together, the cross-validation error indicated K = 5 major groups with fine structure up to K = 11 groups, corresponding largely to the single species analyses (Figure S2c). At K = 2, the parental species were distinguished and hybrids appeared as admixed (Figure S3). The clusters at K = 5 were identical with the combination of the single species clusters at K = 3 for LC and K = 2 for LT (Fig. 3a, d). At K = 11, seven clusters were distinguished in LC in a slightly different manner than in the single species analysis, and four clusters were distinguished in LT as in the single species analysis. Individuals identified as hybrids in the NewHybrids analysis expectedly showed high admixture proportions. The ancestral groups identified corresponded with the geographic distribution and relative isolation of the sampled populations (Fig. 4). Therefore the 11 clusters

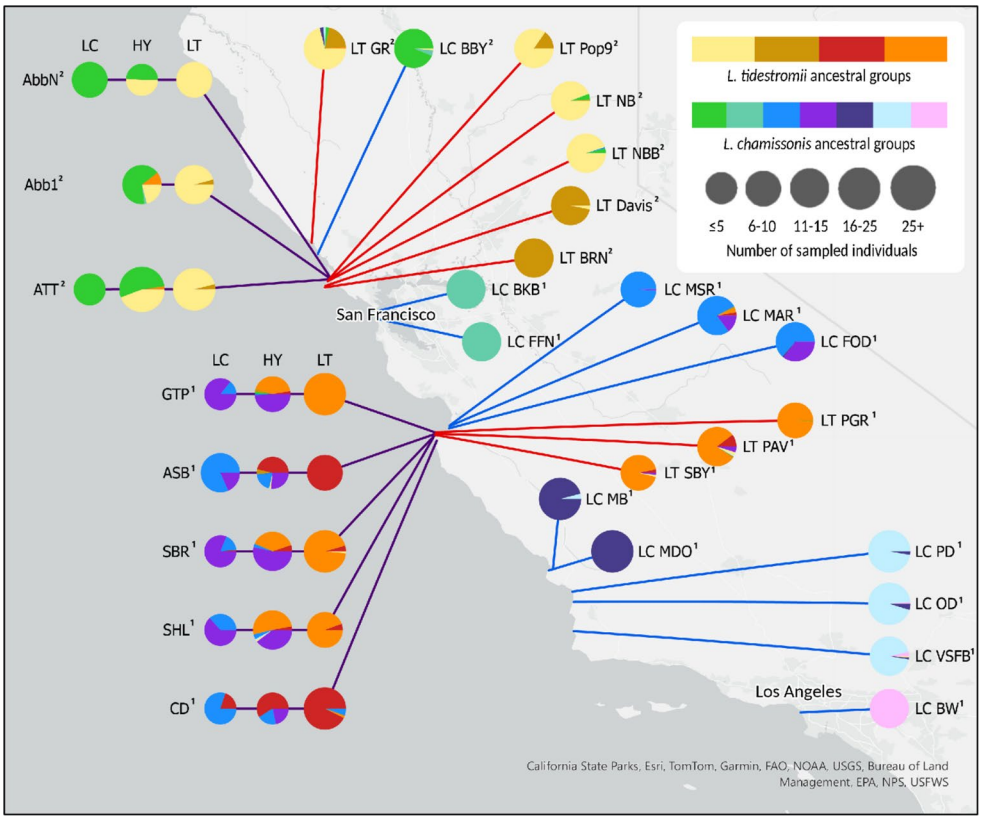


**Fig. 4** Map showing the distribution of ancestral groups from the ADMIXTURE analysis of all individuals for $K = 11$ at the site and taxon level, with *L. tidestromii* shown in brown-red-orange and *L. chamissonis* in blue-green-pink colors. Each pie represents all individuals of a single NewHybrids group aggregated at a single site. Superscripts after site names correspond to cpDNA group assignment. Pie graphs emerging to the right represent sites where only a single species is present, while graphs emerging to the left represent sites of co-occurrence. Sites of co-occurrence are decomposed into three charts per site, indicated by the taxon abbreviation above (excl. site Abb1, where no *L. chamissonis* were sampled). Line colors correspond to the site's species composition: red = *L. tidestromii* only, blue = *L. chamissonis* only, violet = co-occurrence. Pie graph colors correspond to ancestral groups for $K = 11$ in Figure S3. Relative size of the pie graphs corresponds to the number of individuals in that category. Note, however, that frequency of hybrids is based on non-representative sampling; see Methods section detailing sampling scheme

distinguished by ADMIXTURE analysis are considered as the natural populations in further analyses. The sites contained within each natural population are presented in Table 3.

**Chloroplast haplotype analysis** Analyzing only the 33 cpDNA SNP markers revealed that all individuals clustered in two cpDNA groups, representing two maternal lineages (Figure S5). These two maternal lineages were present in both L. tidestromii and L. chamissonis. However, mapping the maternal lineages on the PCA of the whole data set revealed that the two lineages largely coincide with the latitudinal separation in a northern and a southern region in both species and go along with the strong intraspecific split in both species (Figs. 2 and 4, S7). In L. tidestromii, populations from the Monterey region represented cpDNA group 1, whereas populations from Northern California represented cpDNA group 2 throughout. In L. chamissonis, most populations represent cpDNA group 1, but three populations in Northern California (AbbN, ATT, BBY) were cpDNA group 2. Thus, when the two species co-occurred on the same sites, they shared the same cpDNA grouping. Consequently, hybrid individuals had the cpDNA group of the paternal species of the respective site (Table S1). A single population of L. chamissonis harbored both cpDNA groups (southernmost site BW).

## Genetic diversity

Descriptive statistics of genetic diversity are given in Tables 2 and 3, and S2. At the species level, expected and observed heterozygosities were lowest in *L. tidestromii*, intermediate in *L. chamissonis*, and highest in hybrids (Table 2). Private alleles analysis at the species level (excluding hybrids) revealed 47 alleles unique to *L. chamissonis* and 330 alleles unique to *L. tidestromii*.

The populations with the lowest expected and observed heterozygosities were the *L. tidestromii* populations in

**Table 2** Taxon-level population genetics statistics. Individuals were pooled by taxon for analysis. Private alleles analysis was conducted at the pooled species-level and excluded all hybrid individuals

| Taxon | *N* | $H_E$ | $H_O$ | Private alleles |
|---|---|---|---|---|
| *L. tidestromii* | 215 | 0.11 | 0.06 | 330 |
| *L. chamissonis* | 203 | 0.24 | 0.13 | 47 |
| Hybrids | 114 | 0.31 | 0.3 | NA |

*N* number of individuals assigned to this taxon by NewHybrids analysis out of 532 total sampled individuals, $H_E$ expected heterozygosity, $H_O$ observed heterozygosity, $F_{IS}$ inbreeding coefficient

**Table 3** Natural population-level population genetics statistics. Heterozygosities ($H_E$, $H_O$) and inbreeding coefficient ($F_{IS}$) were calculated as weighted means of the sites contained within each natural population. All values of $F_{IS}$ are non-significant ($p > 0.01$). Private alleles analyses were performed on species-specific subsets of individuals which excluded hybrids. Natural populations are grouped by region

| Population | Sites contained | *N* | $H_E$ | $H_O$ | $F_{IS}$ | Private alleles |
|---|---|---|---|---|---|---|
| LT PRNS N | GR, AbbN, Abb1, ATT, Pop9, NB, NBB | 94 | 0.041 | 0.053 | −0.111 | 95 |
| LC N | BBY, AbbN, ATT | 25 | 0.095 | 0.107 | −0.044 | 16 |
| HY N | GR, BBY, AbbN, Abb1, ATT, NB, NBB | 61 | 0.242 | 0.305 | −0.122 | NA |
| LT PRNS S | Davis, BRN | 24 | 0.041 | 0.054 | −0.13 | 11 |
| LC SFO | BKB, FFN | 24 | 0.125 | 0.136 | −0.018 | 5 |
| LC MON A | MSR, MAR, FOD, ASB, CD | 47 | 0.119 | 0.121 | 0.037 | 9 |
| HY MON A | MSR, ASB, CD | 11 | 0.231 | 0.313 | −0.095 | NA |
| LT MON A | ASB, CD | 26 | 0.052 | 0.065 | −0.088 | 16 |
| LC MON B | GTP, SBR, SHL | 7 | 0.132 | 0.151 | 0.108 | 19 |
| HY MON B | GTP, PAV, SBY, SBR, SHL | 42 | 0.25 | 0.292 | −0.068 | NA |
| LT MON B | PGR, GTP, PAV, SBY, SBR, SHL | 71 | 0.063 | 0.07 | −0.014 | 152 |
| LC SLO | MB, MDO | 38 | 0.132 | 0.142 | −0.011 | 8 |
| LC S | PD, OD, VSFB | 50 | 0.149 | 0.158 | −0.002 | 12 |
| LC LA | BW | 12 | 0.123 | 0.124 | 0.052 | 2 |

*N* number of individuals assigned to this taxon by NewHybrids analysis out of 532 total sampled individuals, $H_E$ expected heterozygosity, $H_O$ observed heterozygosity, $F_{IS}$ inbreeding coefficient, *LTLupinus tidestromii*, *LCLupinus chamissonis*, *HY* hybrids of *L. tidestromii* and *L. chamissonis*, *PRNS* Point Reyes National Seashore, *SFO* San Francisco, *MON* Monterey, *SLO* San Luis Obispo, *LA* Los Angeles

See Table 1 for site abbreviations

the north (LT PRNS N, LT PRNS S; Table 3). Inbreeding coefficients were not significantly different from zero at any population or site (Table S2). When performed on only individuals of the same species, private alleles analyses revealed low numbers of alleles unique to each population or site for *L. chamissonis* and higher numbers of alleles unique to each population or site for *L. tidestromii* (Table 3, S2). From a conservation perspective, it is important to note that the southern populations at PRNS have much fewer private alleles than in the northern populations at PRNS.

Hierarchical AMOVA showed that most variation was observed between taxa (51% with hybrids, 58% without hybrids), with moderate variation observed among regions (40.8% with hybrids, 33.5% without hybrids), and low variation observed among natural populations, among sites, and within sites (all less than 8%; Table S3). Considering only *L. chamissonis*, most variation was observed among regions (66.5%) and moderate variation was observed among natural populations (24%) and among sites (13%), with essentially no variation observed within sites (<0%, considered 0%). Considering only *L. tidestromii* individuals, nearly all variation was observed between regions (98%), with little variation observed among natural populations, among sites, and within sites.

Overall differentiation between *L. tidestromii* and *L. chamissonis*, calculated as $F_{ST}$ of all pure-species individuals, was $0.654 \pm 0.015$ ($p < 0.001$). Differentiation at the regional level was higher in *L. tidestromii* (two regions, $F_{ST} = 0.67 \pm 0.025$, $p < 0.001$) than in *L. chamissonis* (three regions, mean $F_{ST} = 0.43$,$p < 0.001$). Differentiation among sites was more extreme within *L. tidestromii* than within *L. chamissoni* (Figure S9a, b). For both pure species, within-region $F_{ST}$ values were lower than between-region $F_{ST}$ values, but within-region $F_{ST}$ values were higher in *L. chamissonis* than in *L. tidestromii*, and between-region $F_{ST}$ values were higher in *L. tidestromii* than in *L. chamissonis* (Figure S9c).

Linear regressions of $F_{ST}$ as a function of pairwise geographic distance revealed a significant relationship in both *L. tidestromii* ($r = 0.955$, $p = 0.002$; Fig. 5a, black line) and *L. chamissonis* ($r = 0.7464$, $p = 0.001$; Fig. 5b). However, excluding between-region comparisons (sites at a distance greater than 100 km apart) in *L. tidestromii* showed no pattern of within-region isolation-by-distance ($r = 0.15$, $p > 0.05$; Fig. 5a, grey line).

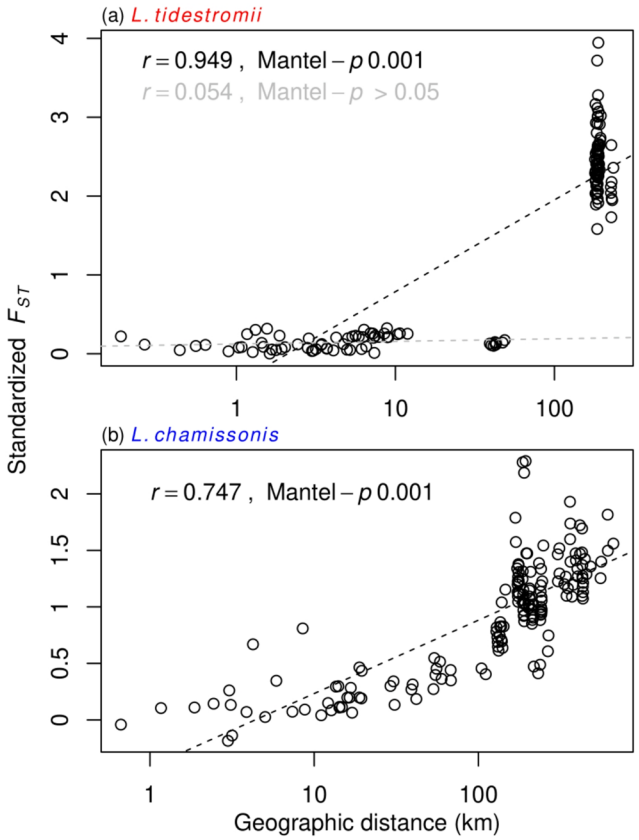


**Fig. 5** Scatterplots of linear regression analyses of pairwise population-level standardized $F_{ST}$ ($F_{ST}$/1 - $F_{ST}$) as a function of $\log_{10}$ pairwise geographic distances in *L. tidestromii* (**a**) and *L. chamissonis* (**b**). Black lines indicate statistically significant relationships indicating isolation-by-distance for the entire datasets. The grey line indicates the non-significant relationship in *L. tidestromii* for within-region comparisons (sites less than 100 km apart)

Linear regressions of $H_O$ and $F_{IS}$ as functions of population size in *L. tidestromii* found no significant relationships between observed heterozygosity (Figure S10a) or inbreeding coefficient (Figure S10b) and population size.

### Hybridization

Hybridization was confirmed at all sites where sympatry was expected. Additionally, hybridization was observed at seven sites where only one species was expected to occur but which were within 1 km of a site of modern or historical sympatry. Table 4 summarizes the historical, expected modern, and observed taxon compositions of each site.

Only three sites (Davis, BRN, PGR) where *L. tidestromii* was sampled showed no evidence of hybridization with *L. chamissonis*. Of these sites, Davis and BRN form the LT PRNS S natural population (dark yellow in Fig. 3), making this the only *L. tidestromii* natural population where hybridization was not observed, while PGR belongs to the LT MON B natural population. At all other sites in the LT MON B natural population, hybridization with *L. chamissonis* (LC MON B) was detected.

At nine sites where *L. chamissonis* was sampled, there was no evidence of hybridization with *L. tidestromii*. These sites included all sites in Southern California where *L. tidestromii* does not occur, the two sites in San Francisco forming the natural population LC SFO where *L. tidestromii* is also not known to occur, and two sites in the natural population LC MON A (MSR, FOD). At all other sites in the LC MON A natural population, hybridization with *L. tidestromii* (LT MON A) was detected. Finally, hybridization between LT PRNS N and LC N was also detected.

## Discussion

Understanding the population genetics of species of conservation concern is an important step in developing impactful management plans, especially when proposed management involves seed translocation. This study aimed to characterize the population genetics of the endangered *L. tidestromii* and its more common congener, *L. chamissonis*, with which it hybridizes to better inform future management decisions. We found evidence of hybridization at all sites where both species occur. The genetic patterns in this study reflect a history of human activity, which resulted in species introductions and local extirpations.

The presence of hybrids at non-sympatric sites is likely due to human activities in the past. For example, the presence of hybrids at the site BBY that was thought to only have *L. chamissonis* provides evidence of a historical population of *L. tidestromii* which has gone extinct in the last 45 years (see footnote in Table 4). This could be due to the intentional planting of dune-stabilizing exotic species in the 1930's that resulted in the destruction of early-successional habitat, and may have resulted in the local extirpation of *L. tidestromii* (C. Heintzelman, personal communication 2024). A similar situation seems to have occurred on the interior of the Monterey Bay, where hybrids were detected at MAR and FOD. A small population of *L. tidestromii* was seen at the nearby site MSR in 2020 but was not relocated during sampling in 2023 (P. Regan, personal communication 2023). These plants may have been wiped out by a large storm and subsequent sand burial, or otherwise succumbed to demographic stochasticity. Conversely, hybrids are present at populations on the Monterey Peninsula that were thought to only have *L. tidestromii. Lupinus chamissonis* was introduced to the Monterey Peninsula starting in the 1960's, and when it was discovered that this species was hybridizing with *L. tidestromii* in the early 2000's, efforts were made to remove *L. chamissonis* from a number of sites (PAV, SBY; T. Moss, personal communication 2024). The

**Table 4** Histories of co-occurrence of *L. tidestromii* (LT), *L. chamissonis* (LC) and hybrids (HY) across sampling sites where hybrids were detected. Taxa are considered "nearby" if they occur within 1 km of the sampled site

| Site | Sampled taxa | Modern expected taxa | Historical expected taxa | Nearby taxa |
|---|---|---|---|---|
| Northern California | | | | |
| GR | LT, HY | LT | LT | LC[a] |
| BBY | LC, HY | LC | LT[b], LC | |
| AbbN | LT, LC, HY | LT, LC, HY | LT, LC, HY | |
| Abb1 | LT, HY | LT, LC, HY | LT, LC, HY | |
| ATT | LT, LC, HY | LT, LC, HY | LT, LC, HY | |
| NB | LT, HY | LT | LT | LC[†] |
| NBB | LT, HY | LT | LT | LC[†] |
| Monterey | | | | |
| MSR | LC | LC, HY | LT[c], LC | |
| MAR | LC, HY | LC | LC | LT (MSR, historical)[c] |
| FOD | LC, HY | LC | LC | LT (MSR, historical)[c] |
| GTP | LT, LC, HY | LT, LC, HY[d] | LT[e] | |
| PAV | LT, HY | LT[f] | LT[e] | LC, HY (ASB) |
| ASB | LT, LC, HY | LT, LC, HY[d] | LT[e] | |
| SBY | LT, HY | LT, HY[g] | LT[e] | LC, HY (SBR) |
| SBR | LT, LC, HY | LT, LC, HY[d] | LT[e] | |
| SHL | LT, LC, HY | LT, LC, HY[d] | LT[e] | |
| CD | LT, LC, HY | LT, LC, HY[d] | LT[e] | |

[†] LC occurs at a distance greater than 1 km from these sites at ATT

[a] LC was recorded nearby in 2017 (Damian Popovic. 2018. iNaturalist observation: https://www.inaturalist.org/observations/16170470. Accessed on 27 May, 2024.) and 2020 (Elizabeth Dougherty. 2021. iNaturalist observation: https://www.inaturalist.org/observations/67834377. Accessed on 27 May, 2024.)

[b] LT was collected nearby in 1980 (Pacific Union College (2024). PUA - Pacific Union College Herbarium. Occurrence dataset https://doi.org/10.15468/24chj5 accessed via GBIF.org on 2024-05-27. https://www.gbif.org/occurrence/3320766825), but the authors were unable to confirm the identity of this specimen

[c] LT was seen at MSR in 2020 (P. Regan, personal communication, 2024), but was not relocated in 2023

[d] Following the introduction of LC to the Monterey Peninsula in the 1960's, hybridization between LT and LC was observed in the 1990's and confirmed in 2000 (T. Moss, personal communication, 2024)

[e] LC was introduced to the Monterey Peninsula starting in the 1960's. No records of LC on the Monterey Peninsula exist before the introduction, so these sites would've historically only had LT

[f] Continued management of this site targeting the removal of LC individuals was suspected to keep the population relatively pure (P. Regan, personal communication, 2023)

[g] Management targeting the removal of LC individuals at this site diminished following changes in staffing (T. Moss, personal communication, 2024), but it was suspected that LC had not reestablished. However, the close proximity to known occurrences of LC meant that continued hybridization was likely

See Table 1 for site abbreviations

detection of hybrids at PAV and SBY indicates that management activities were insufficient to undo the effects of introduction. As no records of *L. chamissonis* on the Monterey Peninsula exist prior to the 1960's, it is likely that all hybridization between *L. chamissonis* and *L. tidestromii* in this region is the direct result of the breakdown of the geographic barriers preventing hybridization due to human activity. For the remaining three non-sympatric sites where hybrids were detected (GR, NB, NBB), pollen transfer from nearby naturally-occurring populations of *L. chamissonis* likely explains the observed incidences of hybridization (see footnotes in Table 4).

Surprisingly, both species showed strong intraspecific regional differentiation in a northern and southern group, which largely coincided with two cpDNA groups that likely represent chloroplast haplotypes shared between the species. However, these splits are additionally supported by many nuclear SNP markers. We hypothesize that the ancestral population was polymorphic for the different cpDNA groups (Figure S8). This polymorphism was maintained after the species split into *L. chamissonis* and *L. tidestromii*. Thereafter, in both species a geographic split into northern and southern subpopulations occurred. This split went along with parallel lineage sorting of chloroplast haplotypes in the southern part for both species and in the northern part for *L. tidestromii* while the northern population of *L. chamissonis* remained polymorphic, but eventually became sorted at site level, ultimately leading to populations monomorphic

for chloroplast groups. The single case where the two chloroplast groups were found in the same site may represent either ancient polymorphism or a genotyping error of that single sample.

At the regional scale, both species showed high genetic differentiation between regions, which is driven by phylogeographic history of increased isolation and the loss of gene flow between regions due to human activities. Urbanization along the coast of California has increased over the past few decades, and exotic species such as *Ammophila arenaria* and *Carpobrotus sp*. were introduced to stabilize coastal dune ecosystems (USFWS 1998). These activities resulted in isolated populations of dune lupines that have become genetically differentiated over time due to the combined effects of dispersal limitation, genetic drift, and, potentially, local adaptation (Loveless and Hamrick 1984).

At the species scale, genetic diversity was low in both studied species compared to similar studies of *Lupinus* species using SNPs (Turner et al. 2018; Huaringa-Joaquin et al. 2023). However, minor allele frequency filtering thresholds strongly influence the values of genetic diversity: higher thresholds filter out low-diversity loci and lead to lower heterozygosities. The low genetic diversity in the studied species could be due to demographic processes such as low overall population sizes, or bottlenecks due to life in dune habitats, which are naturally prone to frequent disturbances. Anthropogenic pressures would amplify the effects of natural disturbances and lead to even lower genetic diversity. Alternatively, the low genetic diversity in the studied species could be explained by the low spatial and temporal climatic variability of the Mediterranean dune ecosystem, as populations experiencing high temporal and/or spatial climatic variation are known to maintain higher levels of genetic variation (Nadeau et al. 2017). In addition, the self-compatible breeding system may contribute to low diversity levels and thus calls for additional studies of outcrossing rate and gene flow distances. Approaching the conservation of at-risk species, comparison of the population genetics of a rare species with a more common congener provides necessary context to assess the relative genetic diversity of the system. Across all sites in the present study, populations of the rare *L. tidestromii* had lower expected heterozygosities than the more common *L. chamissonis*, as expected (Gitzendanner and Soltis 2000; Boyd et al. 2022). Additionally, while both species exhibited high regional genetic differentiation, the regional differentiation in *L. tidestromii* was even slightly higher than differentiation between species. High among-region variation in *L. tidestromii* indicates that these regions have been isolated for a long time (e.g., Daco et al. 2019). Coupled with the cpDNA analysis, which indicated shared ancestry between these species common within each region, these results support the taxonomic distinction of the two morphologically-distinct regional varieties of *L. tidestromii* (Eastwood 1938; Howell 1986; Riggins and Sholars 1993) and raise the question of whether to elevate these varieties to the species level. Broader phylogenetic analysis of this clade should be performed to better understand the evolutionary relationships among these taxa and provide further context to best support conservation of *L. tidestromii*.

In *L. tidestromii*, intraregional population structure contributed much less to the overall population structure than in *L. chamissonis*. It is likely that any differentiation between sites or populations of *L. tidestromii*, especially within the PRNS region, is due to genetic drift rather than local adaptation, considering that *L. tidestromii* is highly specialized on early-successional microhabitats (Pardini et al. 2015). In early-successional dunes, dynamics of sand burial are the most important drivers of community assembly and serve as a stronger selection pressure independent of other abiotic factors such as soil chemistry, which is known to vary between populations of *L. tidestromii* (Maun 1998; Coppoletta 2005). The greater role of genetic drift is further supported by the private alleles and ADMIXTURE analyses, which suggest that the LT PRNS S natural population is more or less a subset of the LT PRNS N natural population, possibly due to the reduced gene flow between these areas following the loss of spatially intermediate populations.

In *L. chamissonis*, our analyses indicated that there was less differentiation between regions and more within-region substructure than in *L. tidestromii*, and all populations of *L. chamissonis* also had fewer private alleles. Together, these results suggest that there is more gene flow occurring across the entire range of *L. chamissonis* than in *L. tidestromii* due to the more even geographic distribution of *L. chamissonis*. It is likely that *L. chamissonis* has a broader environmental niche than *L. tidestromii*, which is evidenced by its much broader geographic distribution (Slatyer et al. 2013; Boyd et al. 2022). A broader niche would allow *L. chamissonis* to occupy habitat that *L. tidestromii* would not find suitable, facilitating a more even geographic distribution compared to the highly-specialized *L. tidestromii*. Higher genetic diversity and the broader ecological niche of *L. chamissonis* may also increase the adaptive potential of this species to changes in environmental conditions that *L. tidestromii* would be unable to cope with (Nadeau et al. 2017; Boyd et al. 2022).

There was no evidence for inbreeding in either species, which indicates that outcrossing is likely preferred over selfing. Like other species of *Lupinus*, *L. tidestromii* exhibits facultative autogamy, wherein self-fertilization can occur in the absence of pollinating bees, but is more effective when a bee visits the flower and "trips" the mechanism to bring pollen in contact with the stigma (Dunn 1956; Karoly 1992; Coppoletta 2005). The floral biology of *L. tidestromii* also

influences the outcrossing rate. Individual flowers open in succession, and each plant only produces a few inflorescences each year, so at any given time, contact with a pollinating bee is likely to introduce pollen from a different individual (Dangremond et al. 2010). Therefore, while *L. tidestromii* is indeed self-compatible, outcrossing rates are likely high enough to prevent inbreeding, drive up observed heterozygosities and in turn reduce the effect of genetic drift. While the breeding system of *L. chamissonis* has not been investigated, it is likely that this species also exhibits some level of self-compatibility coupled with a preference for outcrossing. This high frequency of outcrossing could further support the dissolution of species boundaries, which allowed for hybridization between these species (Ellstrand et al. 1996).

Understanding the effects of hybridization on populations requires information on the population genetic structure of hybridizing taxa, combined with demographic monitoring to assess plant fitness. Hybridization has the potential to be used as a tool to rescue declining species, and can be considered a natural process essential to the maintenance of diversity and ecosystem functioning (Anderson 1953; Chan et al. 2019). Hybridization between *L. tidestromii* and *L. chamissonis* was detected at all sites where both species occur, and at an additional six sites where only one species was expected to be present. We therefore have evidence for both natural and anthropogenic hybridization in this system. In the Northern California region, hybridization is entirely natural. It is likely that species boundaries are only loosely maintained in this region, and incomplete overlap of the habitat preferences and flowering periods serve as the barriers to complete admixture. In the Monterey region, however, hybridization is an anthropogenic process driven by the introduction of *L. chamissonis* onto the Monterey Peninsula. In both regions, the presence of $F_2$ and backcrossed hybrids indicate that hybridization is a bidirectional process. Whether hybridization could therefore confer some of the adaptive potential from *L. chamissonis* to *L. tidestromii* and support this at-risk species is unknown. The process of hybridization is strongly dependent on the relative fitness of hybrid individuals, the demographic dynamics of the population, and the spatial distribution of individuals (Levin et al. 1996; Todesco et al. 2016). In order to best understand the dynamics of hybridization in this system, genetic characterization should accompany long-term monitoring of marked individuals and their offspring in both regions to assess the relative fitness and demographic dynamics of both species and their hybrids. Such approaches were beyond the scope of the present study, and care should be taken to not overinterpret the presented hybridization data as frequencies of hybridization due to our sampling design. Nevertheless, hybridization should not be considered a threat to *L. tidestromii* in the Northern California region due to its status as a natural process.

Based on the results of the present study, we make specific conservation management recommendations for *L. tidestromii*. The presence of hybrids at three sites (BBY, MAR, FOD) provided evidence for recent local extirpations of *L. tidestromii*, and this new information combined with our prior information on the ongoing decline and extinction risk of populations within PRNS (Compagnoni et al. 2021) emphasizes the urgency to conduct management interventions for this species before more populations and genetic diversity are lost. Within PRNS, genetic differentiation between populations is very low, thus we recommend sourcing seed from all of the larger populations (LT PRNS N natural population) to supplement the smaller, declining populations (LT PRNS S natural population). Such an act of within-region assisted gene flow may be the only way to conserve *L. tidestromii* in a changing climate by increasing the genetic diversity and adaptive potential of the declining or small populations (Bucharova et al. 2019). Further, we suggest that habitat restoration, followed by reintroductions of *L. tidestromii* from seeds sourced from LT PRNS N should be conducted at BBY. Similar actions should be considered along the interior of Monterey Bay (sites MAR, FOD, and/or MSR), with seeds sourced from LT MON A. Such conservation actions would increase connectivity across this species' range and further provide a buffer against extinction through increased gene flow (Weeks et al. 2011). The presence of hybrid individuals in *L. tidestromii* populations north of San Francisco should not be interpreted as evidence that this is not a unique species in need of the conservation protections provided by the US Endangered Species Act. Our population structure analyses show clearly that most of the genetic variation across individuals was explained by whether the individual was *L. tidestromii* or *L. chamissonis* (the first PC axes explained 47.1% of the variation).

On the Monterey Peninsula, anthropogenic hybridization is occurring, and all *L. tidestromii* populations are small and at an increased risk of extinction compared to the relatively well-protected populations at PRNS. Thus, a different approach to management might be necessary for the *L. tidestromii* in this region. The strong genetic differentiation between the northern and southern regions found in this study suggests that a taxonomic reassessment of the two varieties of *L. tidestromii* should be conducted in a follow-up study. In any case, the strong genetic differentiation between the regions justifies separate conservation management approaches for the two regions where *L. tidestromii* currently occurs. Due to the high genetic differentiation between the two regions, seeds of *L. tidestromii* sourced from north of San Francisco should not be used for conservation actions in Monterey.

## Conclusions

Population genetics can help inform management decisions for the conservation of rare species. This study provides a rare example of the population genetics of an endangered species in the genus *Lupinus* and a more common species with which it hybridizes across both species' entire geographic ranges, including genetic characterization of nearly every known population of the federally-endangered *L. tidestromii*. Both species exhibit low genetic diversity, with *L. tidestromii* having particularly low levels of expected heterozygosity. We find high genetic differentiation between regions, especially for *L. tidestromii*, whose populations show limited gene flow, likely due to human activities that have resulted in local extirpations and habitat fragmentation. We recommend conservation actions for declining and extirpated populations of *L. tidestromii* in the Northern California region with seeds that are sourced from the larger populations in this region. This recommendation is supported by knowledge that hybridization is natural within this region, that genetic differentiation between populations within this region is low and by the private alleles analyses, which revealed that the small and declining populations have a subset of the alleles present in the larger populations. A different approach might be needed for the Monterey populations of *L. tidestromii*, as the populations are all small and at risk and because hybridization is anthropogenic in this region.

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**Authors' contributions** Eleanor A. Pardini, Lorraine S. Parsons, Tiffany M. Knight and Walter Durka conceived the study. Aspen Workman, Lorraine S. Parsons and Eleanor A. Pardini collected the samples. Stefan G. Michalski and Walter Durka performed the molecular analysis. Aspen Workman, Walter Durka and Stefan G. Michalski performed the statistical analyses and prepared the figures. All authors contributed to the interpretation of the results. Aspen Workman wrote the manuscript. All authors contributed to editing the manuscript and approved the final version.

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**Data availability** Raw sequence data is available from the European Nucleotide Archive (https://www.ebi.ac.uk/ena) under accession number PRJEB72106 and individual sample numbers ERS17855825 - ERS17856375. Data and code are available on Zenodo (https://doi.org/10.5281/zenodo.17713484). Exact individual and site locations were generalized to protect the endangered *Lupinus tidestromii* in accordance with California Department of Fish and Wildlife. Location data can be made available by reasonable request.

## Declarations

**Competing interests** The authors declare no competing interests.

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