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# Effective dispersal patterns in prairie plant species across human-modified landscapes

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## Abstract

Effective dispersal among plant populations is dependent on vector behaviour, landscape features and availability of adequate habitats. To capture landscape feature effects on dispersal, studies must be conducted at scales reflecting single-generation dispersal events (mesoscale). Many studies are conducted at large scales where genetic differentiation is due to dispersal occurring over multiple generations, making it difficult to interpret the effects of specific landscape features on vector behaviour. Genetic structure at the mesoscale may be determined by ecological and evolutionary processes, such as the consequences of vector behaviour on patterns of gene flow. We used chloroplast haplotypes and nuclear genome SNP surveys to identify landscape features influencing seed and pollen dispersal at a mesoscale within the Rogue River Valley in southern Oregon. We evaluated biotic and abiotic vector behaviour by contrasting two annual species with differing dispersal mechanisms; *Achyrachaena mollis* (Asteraceae) is a self-pollinating and anemochoric species, and *Plectritis congesta* (Caprifoliaceae) is biotically pollinated with barochoric seeds. Using landscape genetics methods, we identified features of the study region that conduct or restrict dispersal. We found chloroplast haplotypes were indicative of historic patterns of gene flow prior to human modification of landscapes. Seed dispersal of *A. mollis* was best supported by models of isolation by distance, while seed-driven gene flow of *P. congesta* was determined by the distribution of preserved natural spaces and quality habitat. Nuclear genetic structure was driven by both pollen and seed dispersal, and both species responded to contemporary landscape changes, such as urban and agricultural conversion, and habitat availability.

**KEYWORDS**
gene flow, isolation by resistance, landscape genetics, mesoscale, pollen dispersal, seed dispersal

## 1 | INTRODUCTION

Long-distance dispersal (LDD) events are infrequent yet have substantial consequences for plant populations including the maintenance of genetic diversity, establishment of novel populations and range expansion (Cain et al., 2000; Nathan, 2006; Sheth et al., 2020). Despite our theoretical understanding of the importance of LDD events, estimating total dispersal among populations

is notoriously challenging to determine for several reasons. First, pollen and most seeds are too small and abundant in quantity to observe reliably, and only a subset of diaspores effectively disperse (Howe & Miriti, 2000). Second, because LDD occurs infrequently and over a large area, it is challenging, if not impossible, to monitor all potential source and destination sites (Nathan, 2001). Third, LDD events are often due to random chance, further complicating predicted dispersal trajectories (Higgins et al., 2003; Rogers et al., 2019; Wang & Smith, 2002). Finally, propagules and spores dispersed beyond the established habitat are subject to the influence of landscape heterogeneity and habitat quality, which lessens the accuracy of dispersal models (Damschen et al., 2014; Gorton & Shaw, 2023; Robledo-Arnuncio et al., 2014). Because it is challenging to incorporate the complexity of variables affecting dispersal into observational models, LDD events are often underestimated with conventional ecological methods (Bullock & Clarke, 2000; Nathan, 2006) but can be assessed using genetic methods (Austerlitz et al., 2004; Jones & Muller-Landau, 2008; Twyford et al., 2020).

By nature, genetic methods measure effective dispersal, which is defined as pollen dispersal resulting in the successful fertilization of an ovule that develops into a seed and germinates into a seedling, or seed dispersal resulting in the germination and growth of a seedling (Cruzan & Hendrickson, 2020; Robledo-Arnuncio, 2011). Interpretation of effective dispersal requires consideration of spatial and temporal scales affecting populations (Robledo-Arnuncio et al., 2014; Twyford et al., 2020); for most plants, individual genetic relationships within fine scales (e.g., scale of less than 1 km radius) will be dominated by annual dispersal events (Grasty et al., 2020), while population structure at large scales (e.g., scale of 100 km radius) will be formed by cumulative multi-generational gene flow (Elleouet & Aitken, 2019). Depending on the dispersal ecology of a species, studies conducted at the mesoscale (e.g., scale of 10 km radius) may capture the interface between drivers of dispersal, such as dispersal vector behaviour or landscape features, and evolutionary consequences, such as prolonged gene flow, drift and colonization dynamics (Arredondo et al., 2018; Leimbach-Maus et al., 2018; Schweiger et al., 2004). Mesoscale studies are of particular interest as they coincide with typical management-level scales (Browne & Karubian, 2018; Myers et al., 2004; Williams, 2017), and only a few studies have considered plant landscape genetics at a scale where genetic differentiation is primarily due to contemporary dispersal events (Emel et al., 2021; Rivkin & Johnson, 2022).

Effective dispersal encompasses establishment in a habitat with adequate environmental conditions to allow growth and reproduction (Auffret et al., 2017; Robledo-Arnuncio et al., 2014; Wang & Bradburd, 2014). Local habitat suitability affects demographic attributes, such as immigration rate and population size. Incorporating habitat suitability is becoming more common in landscape genetics, particularly in animal migration studies (Pereoglou et al., 2013; Pflüger & Balkenhol, 2014; Wishingrad & Thomson, 2023). The interaction between the dispersal of mobile organisms and habitat quality has been well-documented, and within- and among-population habitat suitability is often a significant component of dispersal patterns (Chiappero et al., 2023; Lange et al., 2012; Pflüger & Balkenhol, 2014). In comparison, because plants are sessile after dispersal, they are especially dependent on movement into a suitable environment and therefore offer a unique glimpse into the dynamic between habitat suitability and dispersal patterns (Robledo-Arnuncio et al., 2014; Sork et al., 1999). Plants also provide a unique opportunity to identify shifts in dispersal patterns between historical and contemporary contexts. Chloroplast and nuclear genomes experience different rates of mutation (Wolfe et al., 1987), and comparison of these markers may reflect gene flow patterns from distinct temporal periods. Due to the low mutation rate of chloroplast genomes, observed gene flow more likely reflects historic landscapes, while nuclear markers are more influenced by contemporary features.

Contemporary human modification of landscapes through urbanization and agricultural expansion can disrupt both dispersal and establishment of plants (Chase et al., 2020; Emel et al., 2021). Dispersal trajectories are directly influenced by changes in land use regime, and fragmentation reduces the abundance of suitable habitat for plant establishment and germination (Cruzan & Hendrickson, 2020). Biotically and abiotically dispersed plants may exhibit unique responses to these changes. Biotically dispersed plants are expected to be more affected by fragmentation than abiotically dispersed plants, as their communities of biotic dispersers will be limited to fragmented regions (Chase et al., 2020). Fragmentation reduces the likelihood of animals migrating among isolated habitat fragments, which lessens gene flow among populations (Aguilar et al., 2008; Auffret et al., 2017). While abiotic vector behaviour may also be impacted by changes in the landscape surface, such variation in atmospheric turbulence over a recent urban development, abiotically dispersed species are frequently less susceptible to human modification (Ozinga et al., 2009). For all forms of dispersal, an increase in habitat fragmentation may change population genetic diversity. Resulting patterns of dispersal, and consequences for genetic diversity, may depend on the arrangement of natural spaces receiving active conservation or preservation efforts (i.e., source-sink dynamics), such as state or federal parks or wilderness areas. Because human modification introduces stochasticity to effective dispersal patterns, anthropogenic land use should be incorporated into contemporary landscape genetics models.

Dispersal patterns are often described using an isolation by distance (IBD) model, in which probability of dispersal decreases as greater distances, and low-frequency LDD events are present in the kernel tail (Bullock & Clarke, 2000; Katul et al., 2005; Wright, 1943). Isolation by distance models are most reliable in fine-scale homogeneous landscapes that experience consistent conditions for dispersal or large scales at which coalescence relationships dominate genetic structure estimates. At the mesoscale, evolutionary relationships are often faint, and IBD models do not capture spatial variation in landscape features, habitat quality and fragmentation, or dispersal vector behaviour (Arredondo

et al., 2018; Leimbach-Maus et al., 2018; Mateo-Sánchez et al., 2015). In this context, dispersal may be influenced by topographical or land use features, such as land elevation, tree canopy coverage, rivers or streams, urbanization, agricultural conversion and meteorological events (Cruzan & Hendrickson, 2020; Sork & Waits, 2010). As an alternative to IBD models, we can test hypotheses of isolation by resistance (IBR), which are more applicable to complex landscapes than IBD models (Manel et al., 2003; McRae, 2006). Isolation by resistance is based on circuit theory and postulates some landscape features are more favourable to dispersal, while other landscape features constrain dispersal (termed 'conduits' and 'resistors', respectively) (McRae et al., 2008). By comparing landscape features to population genetic differentiation, we can infer how the rate of gene flow fluctuates across heterogeneous landscapes (Chiappero et al., 2023; Leimbach-Maus et al., 2018; Segelbacher et al., 2010; Sork & Waits, 2010).

Here, we explore the effects of heterogeneous landscapes on patterns of seed and pollen dispersal, and consequently gene flow, in two plant species, *Achyrachaena mollis* and *Plectritis congesta*. The comparison between *A. mollis* and *P. congesta* offers unique insight into the different landscape drivers of gene flow. Both species grow within the upland prairie ecoregion of the Rogue River Valley in southern Oregon, which is defined by a patchwork of urbanization, agricultural conversion, conserved public land and the Rogue River system. Historical accounts and aerial photographs indicate urbanization and agricultural development of this region started in the 1880s, suggesting contemporary dispersal has occurred in the context of human-modified landscape features. Cytoplasmic markers are inherited maternally in both forb species, and therefore, we utilized a combination of chloroplast and nuclear markers to separate seed and pollen dispersal responses to different landscape features and contrast historical and contemporary gene flow. While *P. congesta* is often visited by biotic pollinators, *A. mollis* likely experiences infrequent biotic pollinator events. In addition, *P. congesta* does not have any obvious seed dispersal syndrome and is primarily barochoric (gravity-dispersed), and *A. mollis* seeds have anemochoric traits (wind-dispersed). Both are self-compatible annuals that grow in dense patches across the study region. Because both species are annuals, their genetic structure is more likely to exhibit the effects of human landscape modification within the last century due to their shorter generation time.

Within this system, we aim to (1) directly compare the connectivity of abiotically and biotically dispersed plants across a mesoscale, (2) explore the effects of landscape features on genetic structure using resistance analyses and (3) compare seed and pollen dispersal patterns observed using chloroplast haplotypes and nuclear SNPs. We expect biotic dispersal vectors to be more sensitive to heterogeneous landscapes (IBR models) than abiotic dispersal vectors, which will be more sensitive to geographic distance among populations (IBD models). We also expect genetic structure of cytoplasmic haplotypes to be higher than nuclear SNPs, due to less frequent long-distance seed dispersal compared with pollen dispersal.

## 2 | METHODS AND MATERIALS

### 2.1 | Study species and region

*Achyrachaena mollis* (Schauer; Asteraceae) is an annual plant found throughout California and southern Oregon in grassland, prairie and disturbed habitats. Plants produce inconspicuous flowers with yellow petals approximately 2.5–5 mm in length. This species is self-compatible, and a low investment in floral displays and early-development anther dehiscence suggests frequent autogamous crosses. Upon pollination, plants produce seeds with anemochoric attributes including a pappus nearly twice the length of the achene. *Achyrachaena mollis* can produce multiple flower heads at a time, and populations often grow in high densities of individuals.

*Plectritis congesta* (Lindl.; Caprofoliaceae; synonym *Valeriana congesta*) is a native annual whose range includes Washington, Oregon and California, and grows in vernally moist and upland meadows. This self-compatible species has a bright pink to white sub-capitate flower with a nectariferous spur, and the fruit is a dry nutlet, with no apparent dispersal syndrome. *Plectritis congesta* frequently hosts a variety of pollinators, including Hymenoptera and Diptera, with *Bombus* (bumblebees) being the most common visitor (Young-Matthews, 2012). *Plectritis congesta* is estimated to experience outcrossing in up to 70% of reproductive events (Layton & Ganders, 1984).

The two study species were sampled across the Rogue River Valley region near Medford, Oregon, USA, within a 20-km radius study range. The surrounding area is a heterogeneous landscape comprised of a mixed forest of oak, madrone and pine; seasonally wet prairies that sustain vernal pools in the early spring; and agricultural land use including cultivated crops, rangeland pasture, and orchards. *Achyrachaena mollis* can be found in disturbed habitats, and *P. congesta* commonly establishes in seasonally moist grassland habitats common to this region; while these species differ in their preferred habitat niche, several of our populations hosted both species.

A total of 32 unique populations of *A. mollis* were sampled for chloroplast sequencing (cpDNA; Kohrn et al., 2017) and nuclear SNP surveys using Genotyping-By-Sequencing (GBS) methods; 16 populations were included in both cpDNA and GBS sampling, 11 were included in only cpDNA sampling, and 5 were included in only GBS sampling (Figure 1a). For *P. congesta*, 27 populations were sampled for cpDNA and GBS sequencing (Figure 1b). Populations were sampled at varying spatial intervals ranging from 30 m to 25 km apart.

### 2.2 | DNA isolation, library and sequencing

For genetic sampling of populations, fresh leaf tissue was collected in the field from individual plants separated by a minimum of one metre to reduce the chance of collecting highly related or clonal individuals. Tissue was preserved in silica, and DNA was isolated using the Qiagen DNeasy Plant Pro Kit for 96-well plates. The quantity and quality of isolated DNA were assessed using Qubit fluorometric quantification and gel electrophoresis imaging.

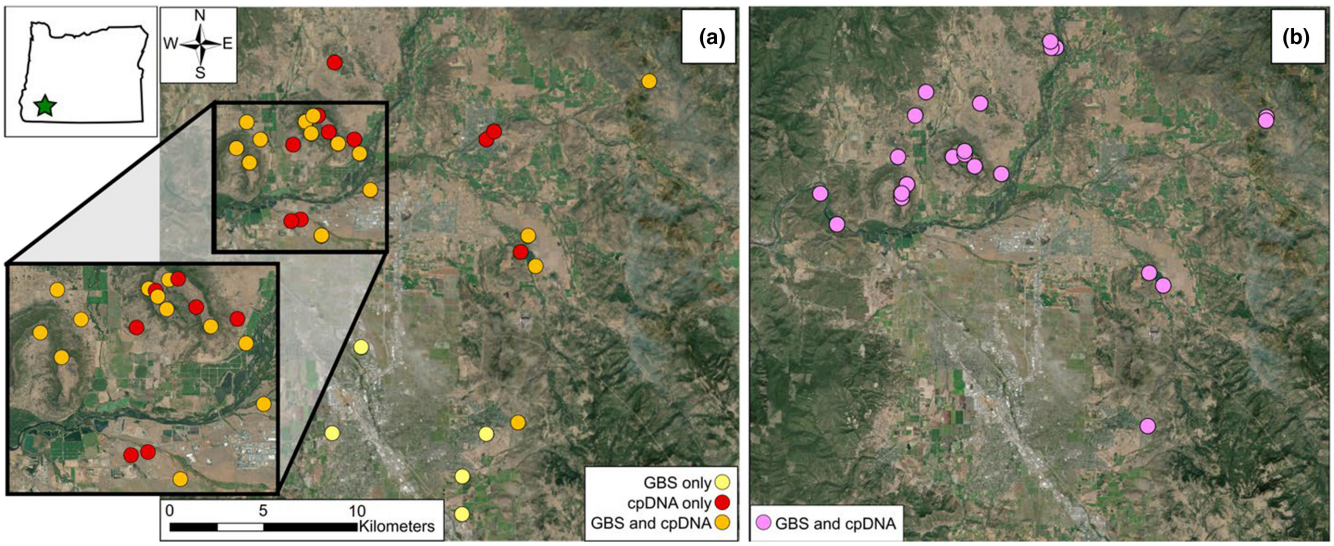


**FIGURE 1** (a) *Achyrachaena mollis* sampling; (b) *Plectritis congesta* sampling. Sampling occurred in the Rogue River region surrounding Medford, Oregon. The colours of the points reference the species and type of sequencing conducted for the population; pink: GBS and cpDNA sequencing for *P. congesta*, orange: GBS and cpDNA sequencing for *A. mollis*, red: cpDNA sequencing only for *A. mollis*, and yellow: GBS only for *A. mollis*.

Whole chloroplast genome sequencing was conducted for both species. Tissue from approximately 20 individuals from each population was collected from the field for DNA isolation. For each unique population, equimolar concentrations of samples were pooled, and a minimum of one sample per population was sequenced individually to separate out population haplotype frequencies from identified SNPs using functions in the CallHap Python package (Kohrn et al., 2017). In-house library preparations using an EcoRI enzyme digest were conducted in accordance with methods provided in Grasty et al. (2020), and 100 bp paired-end sequencing was performed at Oregon Health and Science University on the HiSeq 2500 targeting 100 million reads per capture. Preliminary results using these data were previously presented in Cruzan and Hendrickson (2020).

Genotyping-By-Sequencing methods were employed for both species to identify reduced-representation whole-genome SNPs (referred to as 'nuclear SNPs' from hereon. While this method of sequencing results in a data set composed primarily of nuclear SNPs, it should be noted that a small fraction of cytoplasmic SNPs may also be included). Approximately 5–10 individuals per population were selected to be genotyped with GBS. Paired-end sequencing was conducted by the University Wisconsin-Madison Biotechnology Center on the Nova Seq6000 targeting 250 million reads per plate. Library preparation was performed by the sequencing facility, and a PstI/MspI double digest was used.

## 2.3 | Bioinformatics analysis

The default settings for the CallHap program were used to call SNPs and identify haplotypes from cpDNA sequencing as follows: Adapter and quality trimming was conducted using Cutadapt (Martin, 2011) and Sickle (Joshi & Fass, 2011), using a minimum base quality value of 30. *Lasthenia burkei* (Walker et al., 2014a, 2014b) and *Lonicera japonica* (He & Qian, 2015) were identified as the closest related genomes in the NCBI GenBank for *A. mollis* and *P. congesta*, respectively, and reads were aligned to the reference genome using the Genome Analysis ToolKit (McKenna et al., 2010). SNPs were called using freebayes (Garrison & Marth, 2012), and chloroplast haplotypes were identified using the VCF_Filt and HapCallr functions in CallHap using a minimum read depth of 400 and minimum variant quality of 20.

Nuclear SNPs were quality-filtered and called using the GBS-SNP-CROP pipeline (Melo et al., 2016). Because no closely related reference nuclear genome exists for either species, a subset of 10 individuals per species were selected to build de novo genomes with GBS-SNP-CROP functions. The minimum call rate was set to 75% of individuals, and minimum and maximum read depths were constrained to 5 and 200 reads, respectively. Using TASSEL (Bradbury et al., 2007), the minor allele frequency was filtered to 0.02, and alleles with a heterozygosity frequency above 0.5 were removed to account for sequencing error. The complete scripts for GBS-SNP-CROP and subsequent analyses can be found at https://github.com/cruzan-lab/landscape-genetics.

## 2.4 | Genetic diversity and distance estimates

Due to the expected high degree of selfing and potential for clonal reproduction in *A. mollis*, the clonecorrect function in the poppr R package (Kamvar et al., 2014) was applied to both species to remove any duplicated genotypes. Post-filtering, global statistics, $F_{IS}$, $F_{ST}$, and $H_o$, were calculated using the basic. stats function in the hierfstat R package (Goudet, 2005) to compare genetic diversity between species.

Three genetic differentiation matrices were used in comparison with landscape features: Edward's chord distance and $N_{ST}$ based on chloroplast haplotypes, and Edward's chord distance based on nuclear SNPs. Edward's chord distance ($D_c$) is based upon shared loci and assumes genetic distance is due to drift only (Cavalli-Sforza & Edwards, 1967). $D_c$ was calculated using dist.genpop in the adegenet R package (Jombart, 2008). $N_{ST}$ measures genetic differentiation based upon a haplotype network phylogeny and was calculated using the SPAGeDi program. The correlation between $N_{ST}$ and chord distance (Hardy & Vekemans, 2002) was assessed with a linear regression, and the root mean square error (RMSE) was calculated for $D_c$ values below 0.5 and at or above 0.5 to assess the fit of the model.

Following calling and filtering of nuclear SNPs for each species, population structure software was used to visualize genetic clustering within the sampled region. STRUCTURE (Pritchard et al., 2000) was run using the parallel_structure command in the ParallelStructure R package (Besnier & Glover, 2013). Up to 21 subclusters (k) for *A.mollis* and 26 subclusters for *P.congesta* were evaluated, allowing for each population to be assigned to a unique cluster. STRUCTURE was run with a burn-in of 50,000 and 100,000 iterations over 5 runs. Delta K was used to determine the number of subclusters and verified with mean natural log of probability of K (LnP(K)) to include the possibility of K=1. Structure Harvester (Earl & vonHoldt, 2012) and CLUMPP (Jakobsson & Rosenberg, 2007) were used to filter results and check for cluster assignment biases, and the distruct program was used in data visualization (Rosenberg, 2003). Genetic structure of chloroplast haplotypes was assessed by comparing individual haplotype occurrence and frequency among populations in ArcMap v10.8.1.

## 2.5 | Resistance layer preparation

Multiple landscape features were identified as having a potential influence on dispersal among populations. Often, LDD occurrences are the result of chance and not driven by the primary dispersal vector. Therefore, we also considered variables that may not be directly influenced by the primary pollen or seed dispersal morphology. Variables included in the models were percent tree canopy coverage, elevation, agricultural use (cultivated crops and pasture), roads, urban development, and the Rogue River and other water features (Table 1; Figure 2). Canopy coverage and elevation layers were retrieved from the US Forest Service tree canopy cover data sets for the conterminous United States, and land use was determined using the US Geological Survey National Land Cover Database assessment from 2016. Natural areas experiencing conservation efforts and minimal anthropogenic disturbance were identified using a combination of layers from the Oregon parks and Recreation District. The final layer was filtered to only contain city and state parks, Bureau of Land Management (BLM) boundaries, hiking trails and wetland areas (Table 1). A five-kilometre buffer was drawn around the sampling extent using the minimum bounding geometry and buffer functions in ArcMap. Each resistance layer was imported, clipped and resampled to a 30-m cell size.

**TABLE 1** Source and host website provided for publicly available datasets used in the analysis.

| Feature name | Source organization | Layer title and year accessed |
|---|---|---|
| Agriculture | USGS | National Land Use Cover Database (2016) |
| Canopy coverage | USFS | Tree Canopy Coverage (2011) |
| Development | USGS | National Land Use Cover Database (2016) |
| Elevation | USGS | National Elevation Dataset (2018) |
| Habitat quality | USFS | Tree Canopy Coverage (2011) |
| | USDA | SSURGO Percent Soil Clay for Oregon (2018), SSURGO Percent Soil pH Matter for Oregon (2018) |
| | USGS | National Elevation Dataset (2018) |
| | PRISM | 30-Year Normals for Mean temperature, Minimum temperature, Maximum temperature, Mean dew point temperature (2018) |
| | WorldClim | Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter, Min Temperature of Coldest Month, Max Temperature for Warmest Month, Mean Diurnal Range (2021) |
| Natural areas | OPRD | Oregon State Parks (2023), Natural Areas (2023) |
| | BLM | OR_stewardship (2023) |
| Rivers | USGS | National Land Use Cover Database (NLCD 2016) |
| Roads | ODOT | Oregon Trans Network Public (2018) |

*Note*: The source organization acronyms used below are: United States Geological Survey (USGS), United States Forest Service (USFS), United States Department of Agriculture (USDA), Oregon Parks and Recreation District (OPRD), Bureau of Land Management (BLM), and Oregon Department of Transportation (ODOT).

## 2.6 | Ecological niche modelling resistance layer

Because the use of genetic markers infers effective dispersal rates (Cruzan & Hendrickson, 2020), dispersal and habitat quality must both be considered as potential drivers of gene flow. Some landscape features may induce differing and separate effects on dispersal and population establishment, and therefore are included in both habitat and resistance models.

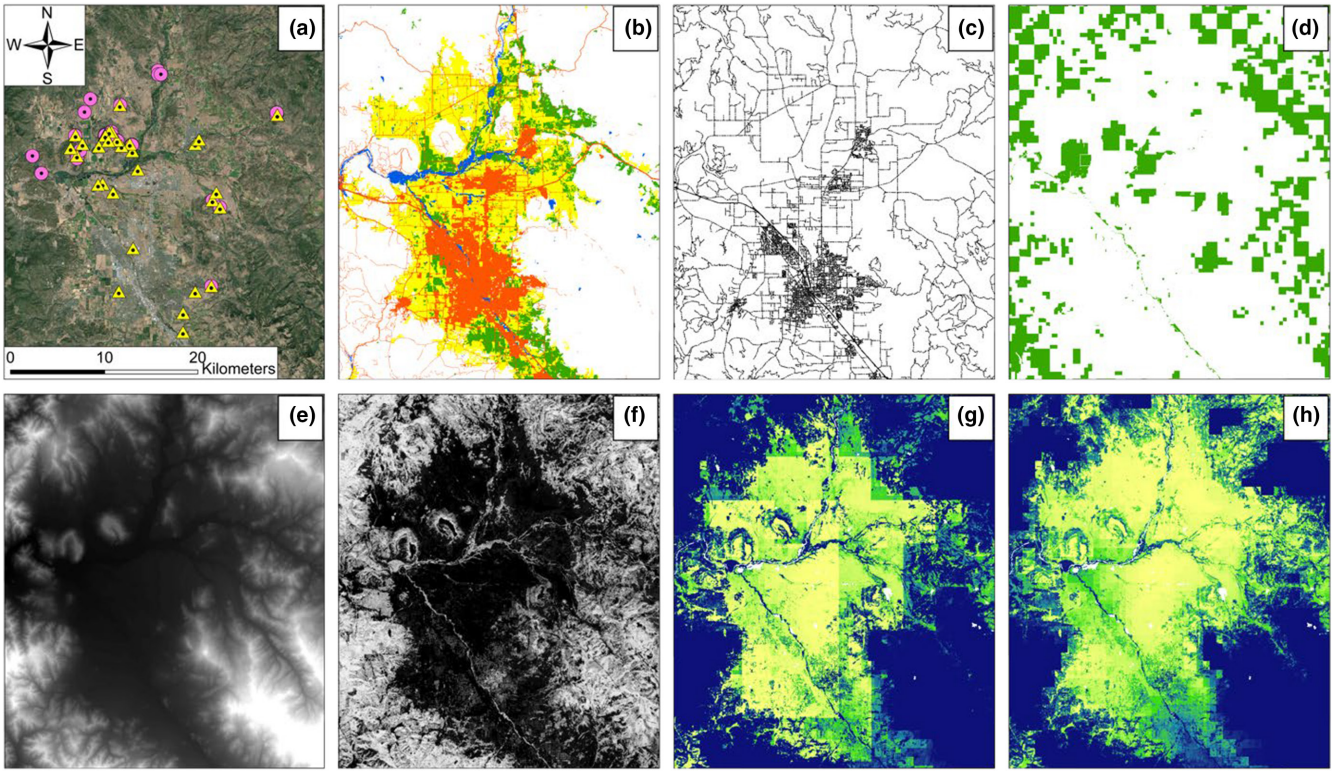


**FIGURE 2** Input layers used for *Achyrachaena mollis* and *Plectritis congesta* optimization in ResistanceGA. (a) Distribution of sampling locations for each species; pink circles represent *P. congesta* populations, and yellow triangles represent *A. mollis* locations. (b) Land use delineation across the sampled area. Red regions are urban development, blue regions are rivers and other water bodies, yellow regions are agricultural land used for hay or grazing pasture, green regions are agricultural land comprised of cultivated crops. (c) Roads across the study region. All roads were weighted equally regardless of road type. (d) Natural spaces consisting of city or state-managed land. (e) Elevation, where darker areas have lower elevation. (f) Tree canopy coverage as reported by the US Forest Service. Lighter areas are more forested while darker areas have less tree canopy coverage. (g) Habitat suitability map for *A. mollis* and (h) *P. congesta* generated using ENMTools.

Habitat quality is estimated using ecological niche modelling (ENM) methods in the ENMTools R package (Warren et al., 2021). A total of 15 environmental parameters were considered including elevation, tree canopy coverage, pH and clay content of soil, and annual temperature and precipitation conditions retrieved from PRISM Climate group (prism.oregonstate.edu) and WorldClim (worldclim.org) (Table 1). Layers were rescaled to 30-m spatial resolution. Any collinear variables were visualized using the raster.cor.matrix() and raster.cor.plot() in ENMTools, and variables with a Pearson's correlation coefficient of greater than or equal to 0.7 were removed, resulting in 11 layers in the final analysis. Occurrence data for each species were based on our previous field observations and supplemented with collections recorded in the Oregon Flora database, resulting in 45 and 35 occurrence points for *A. mollis* and *P. congesta*, respectively. The enmtools.glm() function was used to build a generalized linear model, with 20% of the data withheld randomly, and a maximum of 10,000 iterations. The habitat suitability map generated by this function was imported into ArcMap and cropped to match the generated resistance layers.

## 2.7 | Isolation by distance and resistance analysis

Resistance values were generated for each landscape feature using the ResistanceGA R package (Peterman, 2018). ResistanceGA uses permutation methods to optimize resistance values for landscape layers in response to population genetic diversity measurements among sample locations. All transformations were considered for continuous features (e.g., elevation) and categorical features (e.g., presence or absence of urbanization) were restricted to resistance values between 1 and 500. The CommuteDistance function in the gdistance R package was used to calculate pairwise random-walk commute times. A total of nine layers were compared as single surfaces to population genetic distance: geographic distance, cultivated crops and hay pasture, rivers and other water features, tree canopy coverage, roads, urban development, elevation, natural spaces delineation and habitat quality from ENM analysis. ResistanceGA v.4.2 was run using R v.4.1 in a Linux environment on the Coeus High Performance Computing Cluster at Portland State University.

ResistanceGA also considers the interactions among landscape features in a 'multisurface'. Three multisurfaces were created for each genetic distance type; one multisurface included only features associated with land use categorization (i.e., agriculture, urban development, roads and rivers), one multisurface considered the highest-ranking individual features, and one multisurface combined the highest-ranking individual features and habitat quality. Model selection was based upon AICc values calculated by the ResistanceGA bootstrapping function and performed over 15,000 iterations using a 75% sample selection.

## 3 | RESULTS

### 3.1 | Haplotype and SNP identification

Following processing with the CallHap pipeline, 12 SNPs were discovered for *A. mollis*, which resulted in 13 unique chloroplast haplotypes (Figure 3). A total of 23 SNPs were discovered within *P. congesta* populations, and 22 chloroplast haplotypes were identified (Figure 4).

The GBS-SNP-CROP pipeline identified 15,471 in the *A. mollis* sequencing and 8863 SNPs in the *P. congesta* sequencing. Following minor allele frequency and maximum heterozygosity filtering, a total of 6756 and 4308 SNPs were retained for each species. No SNPs were removed by clonal correction. STRUCTURE analysis determined two subclusters existed within each species, which were equally distributed across all sampled populations (Figure S1; Table S1).

### 3.2 | Genetic diversity and distance measures

All genetic diversity metrics were consistent between species. Global $F_{ST}$ and $F_{IS}$ values based on nuclear SNPs for *A. mollis* were 0.0219 and −0.0247 respectively, and 0.0269 and −0.0429 for *P. congesta*. Global heterozygosity from nuclear SNPs was 0.0864 and 0.0867 for *A. mollis* and *P. congesta*. $D_c$ for nuclear SNPs averaged 0.1593 and 0.1787 for *A. mollis* and *P. congesta*, respectively. $D_c$ for chloroplast haplotypes averaged 0.4805 for *A. mollis* and 0.4740 *P. congesta*; mean $N_{ST}$ values chloroplast haplotypes were 0.2265 and 0.2397.

A significant, positive relationship was found between $D_c$ and $N_{ST}$ based on chloroplast haplotypes for *A. mollis* ($p$-value < .01, $R^2 = .4674$) and *P. congesta* ($p$-value < .01, $R^2 = .6651$). The fit of the model was heteroskedastic, with a tighter fit at small genetic distance values compared with larger distances for both *A. mollis* (RMSE overall = 0.1405, RMSE below 0.5 $D_c$ = 0.0821, RMSE at or above 0.5 $D_c$ = 0.1837) and *P. congesta* (RMSE overall = 0.1524, RMSE below 0.5 $D_c$ = 0.0495, RMSE at or above 0.5 $D_c$ = 0.1733) (Figure 5).

### 3.3 | *Achyrachaena mollis* ResistanceGA model selection

Overall, *A. mollis* gene flow patterns were often correlated with geographic distance (Table 2; Figure 6). When considering chloroplast haplotypes, which reflect seed dispersal only, $N_{ST}$ found geographic distance (AICc = −41.12, $R^2_m = .017$), elevation (AICc = −38.46,

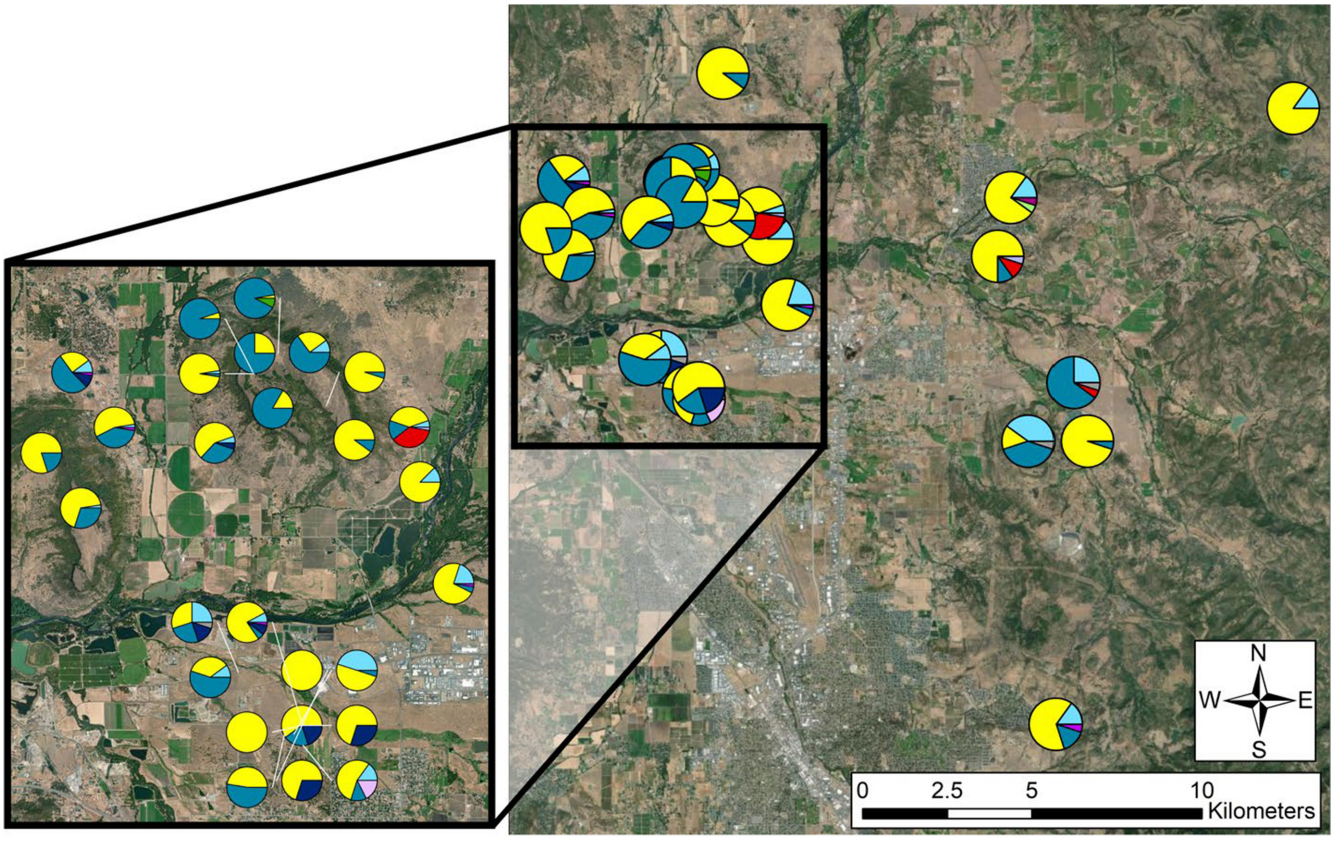


FIGURE 3 *Achyrachaena mollis* population structure as observed within chloroplast haplotypes. Each pie chart represents a population, and each colour within the pie chart represents a unique haplotype. The chart inset depicts fine-scale sampling of *A. mollis*, and the white leading lines indicate the precise sampled location.

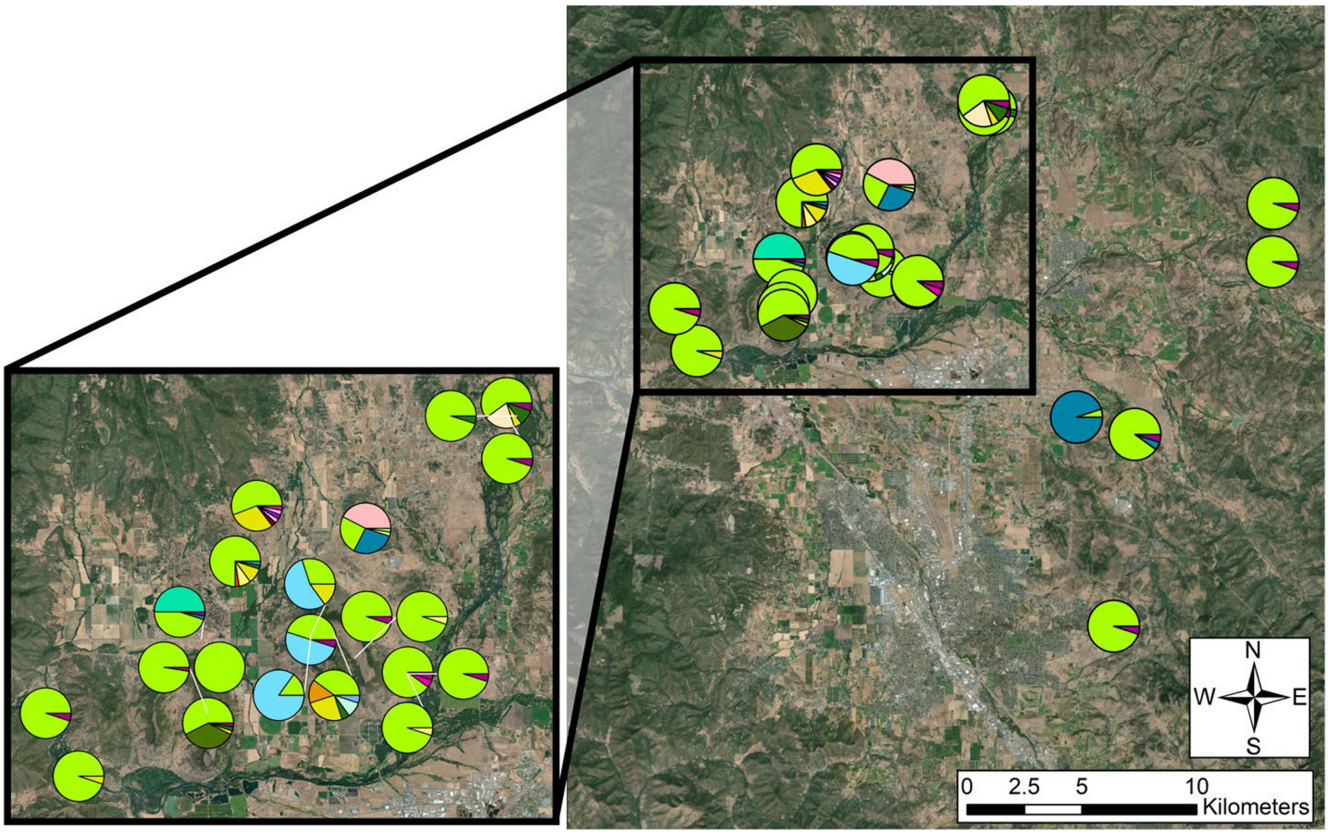


FIGURE 4 *Plectritis congesta* population structure as observed within chloroplast haplotypes. Each pie chart represents a population, and each colour within the pie chart represents a unique haplotype. The chart inset depicts fine-scale sampling of *P. congesta*, and the white leading lines indicate the precise sampled location.

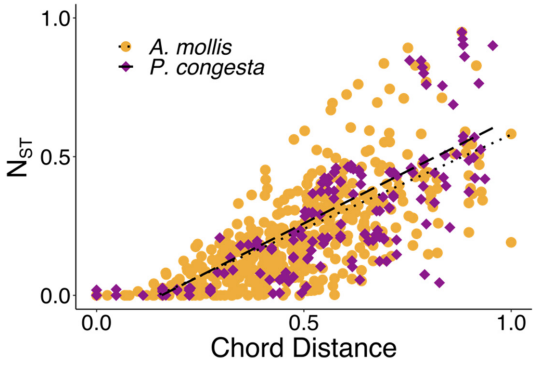


FIGURE 5 Linear relationship between $D_C$ and $N_{ST}$ for *Achyrachaena mollis* (orange; $R^2 = .4674$, $p$-value < .01) and *Plectritis congesta* (purple; $R^2 = .6651$, $p$-value < .01).

$R^2_m = .089$) and agriculture (AICc = −36.99, $R^2_m = .071$) to be the most predictive models, and elevation and agriculture explained more variation than geographic distance. Combined, these models represent 82.6% of bootstrapping iterations. $D_c$ based on chloroplast haplotypes were best predicted by geographic distance (AICc = −66.43, $R^2_m = .041$), natural spaces (AICc = −63.45, $R^2_m = .040$) and rivers (AICc = −63.362, $R^2_m = .045$), which had similar explanatory power. These three models were identified as the best models in 99% of the bootstrapping iterations.

Nuclear SNPs represent both pollen and seed dispersal across the landscape. The best model explaining patterns of $D_c$ based on nuclear SNPs was a multisurface consisting of agriculture and development interactions (AICc = −754.42, $R^2_m = .447$). As explanatory variables, agriculture contributed approximately 78.6% and development approximately 21.4%. Geographic distance was the second most predictive model but explained much less variation (AICc = −761.805, $R^2_m = .009$). These two models were selected during 92% of bootstrapping iterations. All ResistanceGA model selection results for *A. mollis* can be found in Table S2.

### 3.4 | Plectritis congesta ResistanceGA model selection

Patterns of *P. congesta* genetic differentiation were often described by land management classification (Table 2; Figure 6). Natural spaces (AICc = −165.17, $R^2_m = .199$), rivers (AICc = −163.75, $R^2_m = .070$) and habitat quality (AICc = −162.63, $R^2_m = .177$) were most predictive for $N_{ST}$ based on chloroplast haplotypes. These models were selected during 63% of bootstrapping iterations, with geographic distance accounting for an additional 33% of iterations. $D_c$ patterns followed a similar trend and were described best by presence of natural spaces (AICc = −197.20, $R^2_m = .285$) and habitat quality (AICc = −194.79, $R^2_m = .349$). These models

**TABLE 2** Summary of best performing models ranked by weighted AICc in ResistanceGA for both study species and all response variables, including $N_{ST}$ from chloroplast haplotypes (cpDNA $N_{ST}$), Edwards chord distance from chloroplast haplotypes (cpDNA $D_c$), and Edwards chord distance calculated for the nuclear SNPs (Nuc $D_c$).

| Species | Variable | Surface | Avg AICc | Avg $R^2_m$ | Selection (%) | Conduit | Resistor |
|---|---|---|---|---|---|---|---|
| *Achyrachaena mollis* | cpDNA $N_{ST}$ | Distance | −41.12 | .017 | 35.76 | *N/A* | *N/A* |
| *A. mollis* | cpDNA $N_{ST}$ | Elevation | −38.46 | .089 | 32.23 | High elevation | Low elevation |
| *A. mollis* | cpDNA $N_{ST}$ | Agriculture | −36.99 | .071 | 14.58 | Off agriculture, on cultivated crops | On hay pasture |
| *A. mollis* | cpDNA $D_c$ | Distance | −66.43 | .041 | 95.92 | *N/A* | *N/A* |
| *A. mollis* | cpDNA $D_c$ | Natural Spaces | −63.45 | .040 | 0.35 | Off natural spaces | On natural spaces |
| *A. mollis* | cpDNA $D_c$ | Rivers | −63.36 | .045 | 2.73 | On rivers | Off rivers |
| *A. mollis* | Nuc $D_c$ | Agriculture + development | −754.42 | .447 | 65.88 | Off pasture, off crops, on development | On pasture, on crops, off development |
| *A. mollis* | Nuc $D_c$ | Distance | −761.80 | .009 | 25.65 | *N/A* | *N/A* |
| *Plectritis congesta* | cpDNA $N_{ST}$ | Natural spaces | −165.17 | .199 | 38.97 | Off natural spaces | On natural spaces |
| *P. congesta* | cpDNA $N_{ST}$ | Rivers | −163.75 | .070 | 11.38 | On rivers | Off rivers |
| *P. congesta* | cpDNA $N_{ST}$ | Habitat | −162.63 | .177 | 12.21 | Low-quality habitat | High-quality habitat |
| *P. congesta* | cpDNA $D_c$ | Natural spaces | −197.20 | .285 | 29.42 | Off natural spaces | On natural spaces |
| *P. congesta* | cpDNA $D_c$ | Habitat | −194.79 | .349 | 31.43 | Low-quality habitat | High-quality habitat |
| *P. congesta* | cpDNA $D_c$ | Elevation | −190.39 | .269 | 11.59 | Low elevation | High elevation |
| *P. congesta* | Nuc $D_c$ | Distance | −1219.73 | .033 | 55.33 | *N/A* | *N/A* |
| *P. congesta* | Nuc $D_c$ | Canopy | −1218.02 | .109 | 18.41 | Mid tree canopy cover | High and low tree canopy cover |
| *P. congesta* | Nuc $D_c$ | Natural spaces | −1218.45 | .100 | 14.74 | On natural spaces | Off natural spaces |
| *P. congesta* | Nuc $D_c$ | Elevation | −1216.96 | .122 | 9.58 | Mid elevation | Low and high elevation |

*Note*: The Surface column lists the layers included in the model; Avg AICc was used for model selection; Avg $R^2_m$ is the average marginal $R^2$; Selection represents the proportion the model was identified as the best model during bootstrapping; and the Conduit and Resistor categories describe the landscape features of the model that increase or decrease gene flow among populations. Summary statistics for all models are included in Tables S2 and S3.

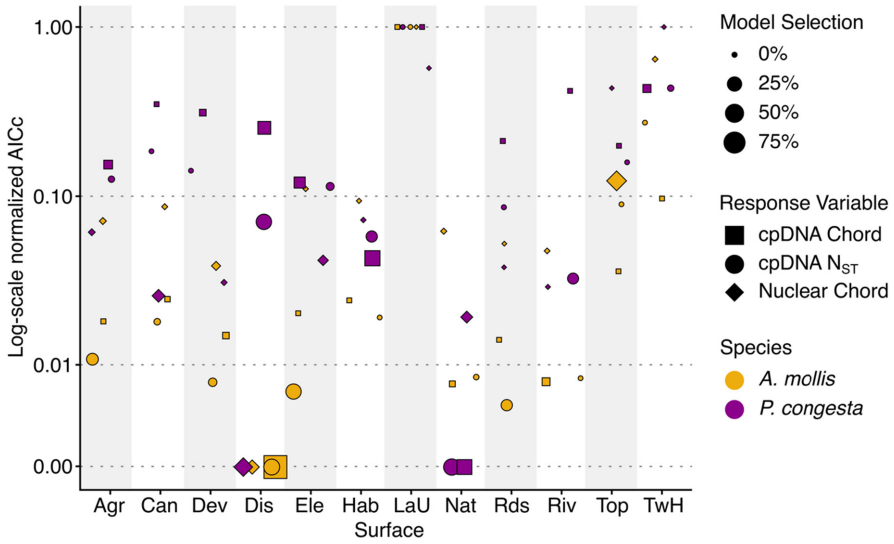


**FIGURE 6** Scatterplot displaying the relationship between the model selection criterion (AICc) and the following resistance surfaces: agriculture classification (Agr); tree canopy coverage (Can); urban development presence (Dev); geographic distance (Dis); elevational gradient (Ele); habitat quality determined by ecological niche modelling (Hab); land use multisurface comprised of agriculture, development, rivers, and roads (LaU); natural space classification (Nat); presence or absence of roads (Rds) and rivers (Riv); multisurface containing the top models during single surface optimization (Top); multisurface containing the top models during single surface optimization with habitat quality (TwH). AICc has been normalized by rescaling between 0 and 1 within each model, where lower values are associated with more predictive models. The size of the point corresponds to how frequently the model was selected during bootstrapping, the shape of the point corresponds to the response variable, and colour indicates species.

were selected 61% of the time during bootstrapping, and geographic distance (AICc = 183.61, $R^2_m$ = .032) was selected 19% of the time.

Gene flow via nuclear SNPs followed similar trends to chloroplast haplotypes. Tree canopy (AICc = −1218.02, $R^2_m$ = .109), natural spaces (AICc = −1218.45, $R^2_m$ = .109) and elevation (AICc = −1218.96, $R^2_m$ = .122) were among the best predictors of genetic differentiation. Geographic distance was found to be a slightly better model but did not explain much variation (AICc = −1219.73, $R^2_m$ = .033). These models represent 98% of bootstrapping model selections. All ResistanceGA model selection results can be found in Table S3.

## 4 | DISCUSSION

At a mesoscale, chloroplast haplotypes were highly structured for both species, while little differentiation was present within nuclear SNP structure, distinguishing the genetic consequences of seed versus pollen movement. Landscape features influencing dispersal varied between species and between chloroplast and nuclear datasets, which indicates the primary vector, sequencing resolution and evolutionary time frame must be considered in effective dispersal studies. Chloroplast haplotype structure of the wind-dispersed species, *A. mollis*, was primarily driven by IBD, with surrounding landscape features exerting little influence over dispersal. However, *A. mollis* nuclear markers were strongly correlated with the agricultural and urban land delineations, suggesting more contemporary dispersal patterns. In contrast, both chloroplast and nuclear genetic structures of the biotically-pollinated species, *P. congesta*, responded to intact or managed natural spaces. Through the comparison between *A. mollis* and *P. congesta*, we can observe the scale and magnitude at which abiotic and biotic dispersal vectors influence population genetic structure, which may inform conservation genetics and management decisions.

### 4.1 | Comparison of $N_{ST}$ and chord distance

Both species exhibited a positive, significant correlation between $N_{ST}$ and $D_c$ calculated from chloroplast haplotypes. While $D_c$ measures the proportion of shared alleles among populations, $N_{ST}$ incorporates phylogenetic relationships based on a haplotype network into distance estimates. A positive relationship between these two metrics is expected, as the greater the phylogenetic separation, the higher the genetic distance. Of note, the model fit changed along the axes, and the relationship was weaker for higher genetic distances. This decrease in fit supported the assumption that distance estimates for isolated populations were more likely to be influenced by mutation accumulation, and therefore, $N_{ST}$ generated from chloroplast haplotypes was expected to consider coalescent-driven similarities among haplotypes, which should improve distance estimates. However, we did not observe a difference between the predictive power (i.e., $R^2_m$) of $D_c$ and $N_{ST}$ in our landscape resistance models, and $D_c$ often outperformed $N_{ST}$. Due to the shortened evolutionary time frame represented within a mesoscale, $D_c$ may be a more reliable genetic distance metric, while phylogenetic metrics (including population genetic structure representations, e.g., STRUCTURE plots) may

not be as sensitive to rare mutational shifts. Our results aligned with those reported by previous studies, which found Euclidian distance to be a robust predictor of genetic structure (Séré et al., 2017; Shirk et al., 2017).

## 4.2 | Population structure and genetic diversity of chloroplast haplotypes and nuclear SNPs

Several factors should be considered when comparing gene flow measured with chloroplast haplotypes and nuclear SNPs. First, the evaluated timescale is directly influenced by genomic resolution and mutation rate between cpDNA and nuclear genomes. The chloroplast genome is one locus, while nuclear data sets can encompass thousands of loci, increasing the opportunity to accumulate mutations among populations and providing more information for robust estimates of distance. Chloroplast genomes are highly conserved and evolve five times more slowly than nuclear markers (Wolfe et al., 1987). Together, these attributes imply any genetic differentiation observed in chloroplast markers is the result of a longer evolutionary timescale than genetic structure measured using nuclear markers, which reflect more contemporary gene flow patterns.

Chloroplast and nuclear mutations encapsulate dispersal at different stages of the plant life cycle. Despite the limitations imposed by low variation in chloroplast datasets, uniparental inheritance of cytoplasmic organelles allows for the direct measurement of gene flow due to seed dispersal separate from pollen contributions (Cruzan & Hendrickson, 2020). In comparison, gene flow estimates based on nuclear SNP variation is comprised of seed and pollen dispersal events, and both propagule dispersal strategies must be considered in the interpretation of results. Pollen frequently disperses farther distances than seeds (Ennos, 1994; Grivet et al., 2009), and previous plant landscape genetic studies often report stronger structure in maternally inherited loci than biparentally inherited markers (Browne et al., 2018; Sork et al., 2015; Tassone et al., 2021; von Takach Dukai et al., 2020).

*Plectritis congesta* and *A. mollis* have disparate reproductive strategies, which affected genetic diversity and structure. *Plectritis congesta* floral and seed morphology suggests a strong investment in outcrossing pollination events and reduced investment in seed dispersal. Genetic diversity among populations supported a low migration rate and large population size, although inbreeding rates were relatively low for *P. congesta* (Appendix S4). Cultivation of *A. mollis* in a controlled environment and dissections across growth stages suggested the species is highly self-compatible, and most seeds were produced by autogamous crosses (unpublished data). Despite the high potential for inbreeding, *A. mollis* individuals did not exhibit increased homozygosity, and no clonality was detected within the sequenced individuals, indicating seeds were not produced by apomixis. Although the inconspicuous flowers of *A. mollis* imply it does not invest in pollinator attraction, rare but impactful outcrossing events and high migration rates among populations (Appendix S4) may accommodate enough gene flow to reach the observed levels of heterozygosity.

Both species exhibited higher genetic structure in chloroplast haplotypes than nuclear SNPs within the mesoscale study range. For *P. congesta*, this pattern was concurrent with genetic diversity and floral morphology observations; high differentiation in chloroplast haplotypes was caused by infrequent, long-distance dispersal events of seeds among nearer populations, while low differentiation of nuclear SNPs inferred pollen and seed dispersal occurred over longer distances and acted as a homogenizing force.

Due to the prevalence of autogamous reproduction in *A. mollis*, a dissimilarity between maternal and nuclear gene flow rates was unexpected, and this disparity highlights the importance of considering the loci resolution in genetic analyses. Although chloroplast haplotypes suggested rare interpopulation seed dispersal events, this pattern diminished when more loci were considered in the nuclear data set, which revealed frequent dispersal among all populations in the range. In context of the low resolution and mutation rate of chloroplast genomes, it is likely structure in chloroplast depicts historical lineages, while nuclear structure provides a more precise model of contemporary dispersal events.

## 4.3 | *Achyrachaena mollis* dispersal trends

Seed morphological attributes indicated *A. mollis* is dispersed by wind, and consequently, we expected this species to be dependent upon landscape features that determine abiotic vector patterns. Anemochoric propagules are subject to wind patterns, and the type of landscape surface determines fluid behaviour. For example, complex surfaces, such as an urban-agricultural matrix, will exert drag, resulting in the loss of energy and allowing seeds and pollen to exit the airstream (Garratt, 1994; Kaimal & Finnigan, 1994). Heterogeneous surfaces will also introduce more turbulence into the flow, a determining factor of seed abscission (Greene & Quesada, 2011; Treep et al., 2018), and will facilitate the movement of seeds higher into the boundary layer, which increases the chance of long-distance dispersal (Horn et al., 2001; Soons & Bullock, 2008). In contrast, fluids passing over homogeneous surfaces, such as a grassland, will be less turbulent, and wind-dispersed propagules will be evenly deposited along the path at greater distances than within heterogeneous landscapes (Nathan et al., 2008).

Because reproduction is primarily autogamous for this species, and very little pollen flow is occurring, contrasting chloroplast and nuclear SNPs provided unique insight into the differences in the timescale of dispersal. Due to the slow mutation rate of chloroplasts, gene flow observed in chloroplast haplotypes represented historic dispersal drivers, while nuclear SNPs reflected contemporary dispersal events, which are more likely to be affected by anthropogenic changes to the landscape. The effect of anthropogenically driven landscape complexity was observed in the comparison of leading models for *A. mollis*. Top-selected models varied by sequencing type, with chloroplast haplotype distribution mostly explained by geographic distance and nuclear SNP structure predicted by an IBR model containing urbanization and agricultural land classification.

The prevalence of IBD models in chloroplast distances reflects historic wind-dispersal patterns across the region, as this region likely consisted of an intact, continuous prairie, which facilitates homogeneous dispersal. In contrast, the strong interaction between nuclear SNPs and the urban-agricultural matrix demonstrated the effects of anthropogenic changes in effective dispersal. Because effective dispersal also encompasses habitat availability, this trend is consistent with *A. mollis*'s preference for disturbed habitats, as development acted as a conduit, and agriculture as a resistor.

### 4.4 | *Plectritis congesta* dispersal trends

In *P. congesta*, patterns of effective dispersal based on nuclear markers were affected by natural spaces, forest canopy coverage and elevational gradients across the sampled region. Due to a higher resource investment in pollinator attraction than seed dispersal vectors, genetic structure was primarily driven by pollen flow rather than seed flow. *Plectritis congesta* is a generalist and is visited by a variety of bee and butterfly species (Young-Matthews, 2012), and dispersal is likely determined by the foraging and habitat preferences of visiting pollinators, some of which can travel tens of kilometres (Goulson, 2010). A recent study by Zitomer et al. (2023) found wild bee abundance and diversity in Oregon decreases with stand age of forested areas, and the widespread anthropogenic disruption in our study region's forests may be exposing *P. congesta* populations to more diverse pollinator communities. In addition, bumble bees, an effective pollinator for *P. congesta*, frequently use forested areas for forage and nesting (Mola et al., 2021), and proximity to these areas may have increased bee visitation rates, causing regions with natural spaces and mid tree canopy coverage to experience higher gene flow rates.

Dispersal of chloroplast haplotypes was dependent on the presence of natural spaces and habitat quality. Because *P. congesta* harnesses biotic methods of dispersal, genetic structure is more sensitive to landscape features, as habitat-driven community composition can induce non-random effective dispersal (Auffret et al., 2017; Damschen et al., 2008). In this study, we found preserved areas of high-quality habitat, such as Bureau of Land Management property or state parks, acted as resistors. While counter-intuitive, there are several explanations for the trend of high dispersal across low-quality environments. First, *P. congesta* seeds do not exhibit any dispersal syndrome, and most seeds are barochorically dispersed close to the parent plant. It is possible *P. congesta* population structure was driven by infrequent LDD events by secondary vectors, such as mammals, which independently respond to landscape features. For example, ungulates, a known browser of *P. congesta* (Skaien & Arcese, 2020), will preferentially forage in areas of high-quality habitat and move rapidly through poorer environments, such as urban regions (Myers et al., 2004), indirectly inflating dispersal across low-quality habitats (Cruzan & Hendrickson, 2020). Additionally, this relationship may be an artefact of genetic sampling for effective dispersal evaluation within habitat fragments. Due to the low mutation rate of chloroplasts, genetic structure likely reflected historic levels of gene flow of populations located within an unfragmented habitat. When intermediate populations are removed, and the distance between intact populations increases, historically high levels of gene flow give the appearance that high-quality habitats experience limited dispersal. In contrast, *P. congesta* nuclear SNPs found natural spaces to be a conduit to gene flow, which likely reflects recent dispersal patterns. This comparison highlights the need to consider the mutation rate of the type of sequencing used in landscape genetics studies.

### 4.5 | Abiotically and biotically dispersed species

The contrast of *A. mollis* and *P. congesta* offers a case study of the ecological and evolutionary consequences of different dispersal mechanisms. The two species were sampled within the same region at comparable frequencies, and both are annuals experiencing similar levels of habitat fragmentation. Yet, gene flow patterns responded to different features of the landscape between species, likely driven by differences in dispersal biology. In general, *A. mollis* experiences higher rates of migration, which is facilitated by abiotic dispersal and a preference for disturbed habitats, while *P. congesta* exhibits lower migration, larger population sizes and a dependence on biotic dispersal. These differences manifest in contrasting IBD and IBR models, with genetic structure of *A. mollis* often associated with the geographic distance gradient, and *P. congesta* frequently associated with landscape resistance.

One of the most notable differences observed between species was the varying dependence on natural spaces. Unlike *A. mollis*, genetic differentiation of *P. congesta* was strongly correlated with the classification of natural spaces. Because both species have similar life histories and experience similar habitat fragmentation, this disparity supports the contribution of dispersal mechanism and habitat preference to plant species' response to anthropogenic change. As an abiotically dispersed species, *A. mollis* is not dependent on local community composition for seed and pollen movement, and human modification further opens novel habitats to *A. mollis*. In contrast, biotically dispersed plants, such as *P. congesta*, are more vulnerable to fragmentation and require the community diversity found in intact natural spaces to facilitate dispersal. Depending on the scale of interest, biotically dispersed plants may require assisted dispersal to establish novel populations. However, once established, animal pollination facilitates adequate levels of dispersal to maintain genetic diversity.

### 4.6 | Dispersal in a mesoscale system

Understanding the ecological and evolutionary consequences of effective dispersal within a meso-scale can be particularly informative in conservation decisions. Mesoscale landscape genetic studies measure annual dispersal events interacting with the contemporary landscape, while large-scale studies often only capture historic

patterns of prolonged gene flow. Therefore, mesoscale studies can inform local groups on conservation and management decisions, such as the optimal locations to establish novel populations to support connectivity, which habitats to prioritize for protection, and landscape features driving populations to genetic isolation.

Our study is one of few to measure plant gene flow among populations at the mesoscale. Within this scale, we identified the historic levels of gene flow among populations, as well as the interaction between plant dispersal ecology and contemporary landscape features. Using chloroplast haplotypes, we found high rates of gene flow within optimal environments, indicative of frequent dispersal over a historically continuous habitat. In contrast, nuclear SNPs represented contemporary rates of effective dispersal, which were driven by the effects of anthropogenic fragmentation. This study demonstrates the extent to which human modification of landscapes influences effective dispersal for biotic and abiotic species, ultimately shaping future genetic structure.

## AUTHOR CONTRIBUTIONS

ECH prepared the manuscript and figures, and designed and conducted bioinformatics pipelines and spatial data analyses. MBC provided feedback and creative input of the manuscript and experimental design, and was responsible for the field sampling and sequencing design, and both ECH and MBC conducted fieldwork and interpreted the results.

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## CONFLICT OF INTEREST STATEMENT

No conflict of interest is declared.

## DATA AVAILABILITY STATEMENT

Metadata are uploaded on Data Dryad (https://doi.org/10.5061/dryad.bnzs7h4h8). Available data include sampling IDs and georeferencing locations, chloroplast haplotype frequencies by population, and filtered nuclear loci files. R and shell scripts used during analysis can be found at https://github.com/cruzan-lab/landscape-genetics.

## BENEFIT-SHARING STATEMENT

Fieldwork was conducted on public and private land with permission from all parties. Neither species are of conservation concern, and plant tissue samples were non-destructively harvested. This project resulted in the training of several undergraduate and graduate students in laboratory and field techniques, whose contributions are outlined in the acknowledgements. The findings described can be informative to local land managers in the study region.

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