

Conservation genomics and species distribution models motivate proactive and collaborative conservation in an era of rapid change

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Abstract

Small, fragmented plant populations with low genetic diversity are susceptible to deterministic and stochastic events that can affect long-term persistence of species. *Penstemon lemhiensis* Keck (Plantaginaceae) is a rare endemic with small, scattered populations across Idaho and Montana threatened by cumulative impacts of biological invasion, drought, and altered fire regimes. When contextualized by an understanding of range-wide distributions under different environmental change scenarios, conservation genetics can be leveraged to motivate proactive conservation action among collaborating stakeholder groups. We applied a genotyping-by-sequencing (GBS) approach across eight populations and 93 individuals of *P. lemhiensis*. Genetic differentiation among populations followed an isolation-by-distance pattern and ranged from low to moderate ($F_{ST} = 0.095\text{--}0.280$). Values of inbreeding were low, and often negative ($F_{IS} = -0.039\text{--}0.032$), indicating outbreeding within populations. Population structure analyses identified six ancestral populations and admixture across all individuals. We contextualized these findings by fitting bioclimatic niche models to past, present, and future climate regime scenarios. Habitat connectivity peaked mid-Holocene and nearly disappeared in the future scenario. Genetic analyses and species distribution models indicated that the species may experience drastic range contraction and accelerated isolation and inbreeding in future. We identified a core area in the Upper Big Hole Valley, Montana most likely to persist as suitable habitat. The National Park Service, Bureau of Land Management, and US Forest Service were identified as key stakeholders in that valley. We outline a proactive collaborative conservation strategy that aim to maintain wild *P. lemhiensis* populations.

Introduction

Earth is experiencing an unprecedented level of biodiversity loss as a consequence of the ongoing Holocene extinction, a series of anthropogenically-driven global extinction events that are threatening > 1 million animal and plant species (Wake & Vredenburg 2008; Díaz et al. 2020). The extinction risk to plant species, which form much of the ecological bases for life, is of particular concern. The greatest threats to plant species include changes in land use (Newbold et al. 2016; Bradley 2010), invasive species encroachment (Vilà et al. 2011), climate related range shifts (Wiens, 2016), habitat degradation and fragmentation (Aguilar et al. 2006), and genetic erosion (Kramer & Havens, 2009). In recent years, plant extinction rates have skyrocketed to 500 times the historic background rate (Humphreys et al. 2019), a value that is likely underestimated due to a lack of comprehensive global assessment of plant species. Proactive and multi-jurisdictional collaborative conservation initiatives and natural resource management strategies that anticipate accelerating changes are required to counteract these drastic losses (Bradford et al. 2018).

Plant conservation efforts receive far less public attention than those of charismatic animal species, despite the essential roles of plants in many ecosystem services (Corlett, 2016). Increased plant diversity and species richness promote overall ecosystem productivity (Cardinale et al. 2011; Hooper et al. 2005), and plants act as ecosystem engineers within many local environments (Espeland & Kettenring 2018).

While a greater proportion of plant species are listed under the federal Endangered Species Act (ESA) than any other taxonomic group, plants receive significantly less conservation funding per species (Negrón-Ortiz 2014), which directly impacts our ability to help them recover (Male & Bean, 2005). The quality of a species recovery plan is also associated with species recovery potential (Stein & Gravuer 2008). Taxonomic bias present in the language of ESA has seeped into aspects of recovery such as plan implementation and revision, critical habitat designation, and more (Clark et al. 2002; Harvey et al. 2002; Hoekstra et al. 2002; Lundquist et al. 2002).

Plant species recovery plans and conservation efforts seldom incorporate or consider genetic factors (Pierson et al. 2016) despite the importance of understanding and preserving genetic diversity (Ralls et al. 2018). The omission of genetic data within conservation initiatives directly reflects the deficit of genetic studies on vulnerable species. Genetic data can be remarkably insightful in elucidating the variation within individual populations (Turchetto et al. 2016) and can be leveraged to understand where state and federal agencies should place conservation priorities (Ahrens & James 2015). Modern genomic approaches allow for discovery of minute patterns of genetic variation within and among populations at low cost. Genotyping-by-sequencing (GBS) is a common genomics approach that has been applied readily over the last decade to understand variation within high diversity groups (Elshire et al. 2011; Ahrens et al. 2017). GBS offers an advantage over other commonly used techniques, such as single sequence repeats (SSRs) and neutral markers, in that it assesses more markers and improves the precision of diversity measurements (Beissinger et al. 2013; He et al. 2014; Narum et al. 2013). GBS has been an essential tool in many population genetics studies (He et al. 2014) and has proven effective in evaluating the genetic diversity of multiple populations of plant species (Fu et al. 2014). Further, in comparison to other PCR or array-based techniques, little prior knowledge of the genome is needed for GBS studies (Poland & Rife, 2012), so it can be readily used in nonmodel species such as those in the genus *Penstemon*.

Penstemon Schmidel, ca. 300 species, (Plantaginaceae) is the largest plant genus endemic to North America (Wolfe et al. 2006). Many species within the genus are rare and restricted to narrow geographic ranges, making them vulnerable to abiotic and biotic threats (Wolfe et al. 2006). The vulnerability within *Penstemon* is well established; 52 species have previously been reviewed for federal listing under the ESA (USFWS 1993), with only *P. haydenii*, *P. debilis*, and *P. penlandii* (USFWS 1987; USFWS 1989; USFWS 2011) officially listed. Previous genetic and demographic assessments of *P. debilis*, *P. albomarginatus*, *P. caryi*, and *P. scariosus* have highlighted high inbreeding coefficients and decreased genetic diversity within isolated populations, increasing their vulnerability to stochastic events (Stone et al. 2019; Rodríguez-Peña et al. 2018; Wolfe et al. 2014; Wolfe et al. 2016). Given the observed vulnerability in genetically assessed species within *Penstemon*, it is clear that further insights on other rare *Penstemon* are warranted.

Penstemon lemhiensis Keck is presently one of many *Penstemon* species of major conservation concern. The largest population resides within Big Hole National Monument, a National Park Service managed protected area in Montana with an estimated 2,500 individuals (Stucki et al. 2013, Rodhouse 2016).

Outside of this area, only three known populations with more than 300 individuals are known (Elzinga 1997). Despite its initial proposal for listing in 1993, the species is not currently listed under ESA, despite initial remarks of declining populations. *Penstemon lemhiensis* is, however, listed as sensitive by both the Bureau of Land Management and the US Forest Service. *Penstemon lemhiensis* does not have sufficient data to infer vulnerability in accordance with the US Fish and Wildlife Service (USFWS, 1993). However, the species is thought to be substantially threatened by interruptions to fire regimes (Heidel & Shelly 2001), encroachment by the invasive spotted knapweed (*Centaurea stoebe*) (Stucki et al. 2013), as well as anthropogenic actions, and increase of drought frequency (Moseley et al. 1990).

Given that *P. lemhiensis* occurs on lands managed by numerous federal, state, private, and non-governmental entities, conservation measures have achieved varied success. To date, several monitoring studies have provided valuable insight into ecological threats to *P. lemhiensis* including competition from invasive weeds and, in the absence of fire or other disturbances, competition from native steppe vegetation (Shelly & Heidel 1995; Heidel & Shelly 1993; Achuf 1992; Shelly 1990). The knowledge gained from this work has led to the testing of conservation management practices in Big Hole National Monument including prescribed fire and use of herbicides to suppress invasive weeds (Stucki et al. 2013; Rodhouse 2016). However, no comprehensive range wide conservation strategy currently exists for *P. lemhiensis*. Additionally, to date, no study has focused on a species-wide assessment of genetic diversity for *P. lemhiensis*. An understanding of the genetic variation within and among populations is essential to evaluating the ability of individual populations to respond to long-term genetic threats such as inbreeding depression (Edwards et al. 2008; Kramer & Havens 2009) and create comprehensive conservation strategies. Given the complexity of conservation management that occurs across a variety of ownership and jurisdictions, the uncertain climate future, and the lack of genetic data about the species, concrete strategies must consider underlying genetic conditions, future scenarios of range dynamics, and address cross-jurisdictional collaboration.

We used the combination of GBS and species distribution modeling (SDM) results to develop a robust conservation management path, identifying a core area within the species' range and stakeholders that can be leveraged for proactive collaborative conservation. Because this study utilizes a GBS approach to infer genetic structure among different populations and subpopulations of *P. lemhiensis*, findings from this study will clarify whether isolation among populations has yet had an impact on genetic diversity. The integration with the SDM analysis provides the context required to then recommend which populations to prioritize for immediate conservation and what a possible future conservation stakeholder network might look like.

Methods

1.1. Study Species

Penstemon lemhiensis is a rare, regional endemic perennial subshrub. that has deep blue-purple flowers with no visible nectar guides (Freeman 2019) and is pollinated primarily by *Pseudomasaris vespoides*

wasps (Ramstetter 1983; Heidel & Shelly 2001). *Penstemon lemhiensis* flowers are protandrous and thus the species is a near-obligate outcrosser (Ramstetter 1983; Elzinga 1997). *Penstemon lemhiensis* is distributed across subranges of the Rocky Mountains in four Montana counties, Beaverhead, Deer Lodge, Ravalli, and Silver Bow, and in Lemhi County, Idaho (Strickler 1997).

1.2. Specimen Sampling and DNA Extraction

Eight sites of *P. lemhiensis*, which we consider as populations within this study, were sampled across Montana and Idaho, along with three subpopulations within Big Hole National Monument in Montana, the most densely sampled area (Fig. 1, Table 1). Leaf tissue was collected in-situ and immediately placed in silica gel. DNA was extracted from dried leaf tissue following the CTAB (cetyl trimethylammonium bromide) protocol (Doyle & Doyle 1991) with modifications (Wolfe 2005). In total, 95 individuals were selected for sequencing. This value is due to both budgetary constraints and low DNA concentration after Qubit DNA quantification assay.

Eight individuals per population are sufficient to accurately estimate population genetic differentiation and genetic diversity parameters (Nazareno et al. 2017). This directly influenced our sequencing protocol. Our sampling strategy aimed to maximize the number of populations at the expense of more individuals because this would allow us to determine changes in genetic differentiation across a larger geographic scale without compromising the demographic estimates (De Mita et al. 2013) and the number of individuals at the expense of depth of genomic coverage (Alex Buerkle & Gompert 2013) as this will yield more accurate estimate of population genetic parameters. We therefore sampled across ten total populations, eight populations and three assumed subpopulations, with eight-thirteen individual each and with an average genomic coverage of 20X per individual. Meaning that, on average, each genetic base or genomic region is represented 20 times.

1.3. GBS library preparation

DNA was quantified via dsDNA fluorometry using Qubit (Thermo Fisher Scientific™, Waltham, MA, USA) and homogenized at 100 ng of DNA per 15 ul. Libraries preparation for genotype-by-sequencing (GBS) follow Elshire et al. (2011). Specifically, to digest the DNA the *Pst*I enzyme (New England Biolabs) was used and unique barcodes were ligated to individual samples before pooling all the samples for PCR. Size selection was carried out in a Blue Pippin (LABGENE Scientific SA) for a range of 200–500. The resulting DNA concentration was determined and fragment size distribution was confirmed using a Bioanalyzer and the Agilent High Sensitivity DNA kit (Agilent Technologies, Inc.). Samples were then sent to Novogene Corporation Inc. for paired-end 150 bp Illumina HiSeq 2500 sequencing.

1.4. Read mapping and variant calling

Quality control of the sequencing data was performed with FASTQC (Andrews 2010). The sequence length was 150 bp and the quality score decreased with sequence length. With FASQC, we also detected the presence of duplicated sequences and adapters. This information was used to inform trimming in the following steps. Samples were demultiplexed and assembled using IPYRAD v0.9.20 (Eaton 2014; Eaton &

Overcast 2020). Default parameters were followed with some exceptions: the maximum number of reads per sample was set to 100,000, samples were trimmed to 50 bp, loci were present in at least 50% of the samples, and the minimum sample per locus was set to the number of individuals per population.

1.5. Population Genetics Analysis

The SNP matrix obtained from IPYRAD assembly was used to estimate basic genetic statistics and population structure. The R package “hierfstat” (Goudet 2005) was used to obtain the observed heterozygosity (H_O), gene diversity (H_S), number of alleles (A), and inbreeding coefficients (F_{IS}) within each population, and to calculate genetic differentiation (F_{ST}) between populations (Weir and Cockerham 1984). The program Arlequin (Excoffier & Lischer 2010) was used to calculate the number of migrants per generation between populations, which was utilized as a measure of gene flow (Serbezov et al. 2012).

Population structure was estimated using ancestry coefficients, a neighbor-joining (NJ) tree, a principal components analysis (PCA), and a discriminant analysis of principal components (DAPC). The goal of using several population structure analyses was to validate the results. Ancestry coefficients were estimated in the R package “LEA” (Frichot & François 2015) which implement the sparse nonnegative matrix factorization algorithms (sNMF) developed by (Frichot et al. 2014). This method is similar to the one implemented in the programs STRUCTURE (Pritchard et al. 2000) and ADMIXTURE (Alexander & Lange 2011), in that they all estimate the ancestry proportion of each individual, but sNMF is more computationally efficient than likelihood algorithms without compromising the accuracy of the estimate (Frichot et al. 2014). We evaluated K 1 to 12 with 10 repetitions per K and used the default for the other parameters. A NJ tree was obtained using the R package “ape” (Paradis & Schliep 2019) which employs the method laid out by Saitou and Nei (1987) to estimate the tree. The PCA were computed using the R packages “adeigenet” (Jombart 2008) and then the individual assignment result from the PCA was used to color the tips of the NJ tree. Finally, the DAPC (Jombart et al. 2010) was run in R and the package “adeigenet” (Jombart 2008), and the function “find.clusters” was used. This function identifies genetic clusters, without prior information about groups, by maximizing the variation between clusters (K-means method).

To determine if the genetic structure of the populations followed an isolation-by-distance pattern, a multiple matrix regression (MMR) analysis was run (Wang 2013). First, the geodesic distance between populations was computed using the package “geosphere” and the function “distGeo” (Hijmans 2019). Then, we followed Wang (2013) and computed an MMR with the between population F_{ST} as dependent matrix and the geographic distance as the independent matrix. Further, the analysis of molecular variance (AMOVA) was used to comprehend the partitioning of genetic variation within and among-populations utilizing R package “ade4” at 1000 permutations.

1.6. Species Distribution Modeling

We used maximum entropy machine learning to estimate the bioclimatic niche of *P. lemhiensis* across its known range during the last glacial maximum (25,000–15,000 year BP), mid-Holocene (6,000 year BP),

present (1980–2010), and future (2070–2099 for a “business-as-usual” carbon emission scenario [RCP 8.5]). We followed methods outlined by Philips et al. (2006) and Elith et al. (2011) to fit models using Maxent (version 3.4.3) software. Presence data (431 geographic locations) for *P. lemhiensis* were obtained from the Montana and Idaho Natural Heritage Programs. Presence data (discrete spatial locations) with acreage amounts of less 4 hectares were classified as having high spatial accuracy (n = 380 geographic locations) and were used in the subsequent modeling. We established an approximation of known range by establishing a 160 km (100 mile) buffer around the convex hull of the species presence data.

Explanatory variables in the model included four biogeophysical and twenty bioclimatic predictor variables (Table S2). Bioclimatic variables were derived (O'Donnell & Ignizio 2012) for 1980–2010 using PRISM normals (PRISM Climatic Group). NASA NEX future projections 30-year normals data were used for 2010–2039, 2040–2069, and 2071–2099 8.5 scenario (NASA NEX). Historical bioclimatic projections for the Mid Holocene and Last Glacial Maximum were obtained from the WorldClim (Fick & Hijmans 2017). Biogeophysical variables, elevation, aspect, slope and northness (Rodhouse et al. 2014), were derived from digital elevation models (NED).

An initial training model with the high spatial accuracy observations (n = 380 geographic locations) and all explanatory variables was modeled for the present time period. A subsequent final variable reduced model was derived for the historic, present, and future time periods using the explanatory variables having a high contribution percentage (≥ 1) in the initial model. We used model output to create binary suitable habitat classifications by assigning the default logistic format output (probability of presence; Elith et. al. 2011) a threshold value of ≥ 0.26 that resulted in a fixed 10% omission rate (Ortega-Andrade et. al 2015).

1.7. Stakeholder Analysis

This study is intended to promote the conservation efforts of *P. lemhiensis*. However, conservation management, broadly speaking, is complex when multiple stakeholder groups with potentially misaligned incentives are required to collaborate (Charnley et al. 2007). This complexity increases in the face of insufficient scientific data. Diverse stakeholders are unlikely to collaborate in the absence of compelling data, and poorly understood or undervalued population dynamics can facilitate potential conservation policy pitfalls due to misconceptions or misinterpretations between stakeholders and sectors.

Given this, an understanding of the genetic structure and distribution of *P. lemhiensis* populations is not sufficient in providing appropriate conservation recommendations. It is also necessary to have a firm understanding of the intricate political and economic relationships as they would affect the conservation of *P. lemhiensis* (Scott et al. 1995). Further, with consideration towards any policy decision, it is critical to understand the central role of stakeholders and their influence on organizational actions (Ramirez 1999). This is particularly necessary for decisions as they pertain to conservation actions (Mushove & Vogel 2005; Welp et al. 2006; Young et al. 2013). To address this, a stakeholder analysis was conducted to

identify and characterize stakeholders and develop a deeper insight into the positions and interests of groups relevant to the conservation of *P. lemhiensis*.

Stakeholders were identified across sectors and characterized based on their respective interest and the power they hold in influencing policy direction as it pertains to conservation management of the species (Bryson 1988; Freeman 1984; Heidrich et al. 2009). This was accomplished through extensive background research and the review of relevant literature, both primary and secondary sources, to understand and assess the influence and interests of organizations. Stakeholders were sorted into four categories – players, subjects, crowd, or context setters – relative to their respective intentions and authority (Ackermann & Eden, 2011). This identifies the players, organizations or individuals whose interest and power should be taken into consideration when addressing key decisions. Data extrapolated from both GIS and the USGS Protected-Areas of the US (PAD-US) database served to elaborate on direct land ownership and management responsibility. Information generated from this analysis will also be beneficial in perceiving current or future opportunities and threats to conservation management. Coupled with the data from SDM, stakeholder information can aid in strategic conservation planning with consideration for future climatic shifts (Bryson 2018).

Results

Estimated population size across the eight populations utilized in this study ranged from 20 to 3000 individuals with 20–31 specimens collected per site (Table 1). The final dataset contained 93 individuals (Table S1), with nine individuals per population for POP1-POP7 and thirty-three for POP8. The SNP matrix consisted of 795 SNPs, 93 individuals and eight populations with a 0.59% missing data, and a total coverage of 848 reads per sample.

2.1. Basic Genetic Statistics and Population Structure

Estimates of population-genetic diversity are summarized in Table 2. The observed heterozygosity (H_o) ranged from 0.09 to 0.13. Similarly, the gene diversity estimates were consistent with H_o such that populations with high values of gene diversity also had high H_o . On the other hand, the number of alleles per population was associated with the number of individuals sampled per population (Table 2). Finally, inbreeding coefficients were low and sometimes negative which is indicative of outbreeding.

The population genetic differentiation followed an isolation-by-distance pattern (Table 3, Fig. 1). The results of the MMR analysis indicated that geographic distance explained 47% of the variation in the genetic differentiation ($R^2 = 0.475$, p-value = 0.0001). In particular, the largest F_{ST} values were found between POP1 and POP6, which are significantly geographically distant populations as well as physically separated by the Beaverhead Mountain Range. The smallest F_{ST} value was found between the two most geographically close populations, POP2 and POP4, approximately six miles apart. Also, the number of migrants per generation (N_m) was consistent with the pattern seen with F_{ST} values such that the highest

values of F_{ST} corresponded to the lowest N_m values. Nevertheless, all populations had N_m values greater than one, which indicates gene flow enough to homogenize the populations (Mills & Allendorf 1996). AMOVA analysis further corroborates detected genetic differentiation; only 15.8% of the total genetic diversity was attributable to diversity among populations, whereas 83.9% of total genetic diversity was attributed to variation among individuals while variation between individuals within populations only amounted to 0.24% of total diversity.

The results from the different population structure analyses used here were consistent with each other. First, the DAPC found seven clusters in the data (Fig. S1); each one representing individual populations, except for cluster five which included two populations, POP2 and POP4. Further, POP3 and POP5 are close together but they form independent genetic clusters. Given the geographic proximity to one another, clustering of these populations is not unexpected. Concurrently with the DAPC, the NJ tree (Fig. S2) shows that all the individuals in POP2 and POP4 formed one group whereas POP3 and POP5 were genetically similar, but similar to the DAPC, formed unique branches in the tree, unlike the relationship seen between POP2 and POP4. Individuals from POP8 were genetically more similar to each other than any other population. That was also evident in the ancestry analysis (Fig. 2) and the PCA (Fig. 3).

Through the ancestry analysis, we were able to identify six ancestral subpopulations (Fig. 2). Overall, while some populations clustered together, we found a heavy degree of admixture across all individuals, despite differences in topography (Fig. 2). The results of the ancestry analysis coincided with both the NJ tree and the DAPC; geographically close populations clustered together while geographically distant populations formed distinct groups. Notably, no major distinctions were detected between the three subpopulations of POP8.

Principal component analysis (PCA) is a valuable statistical tool for analyzing high-dimensional data and has been of particular use in understanding population structure and ancestral variation (Privé et al. 2020). The results of the PCA further complement the results seen in the ancestry analysis, NJ tree, and DAPC. Clustering of populations was largely a factor of geographic distance. As found in previous analyses, POP2 and POP4 clustered together, as well as POP3 and POP5. Unexpectedly, POP1, POP7, and POP8 clustered together in the PCA, despite significant geographic distance and the presence of physical barriers between populations.

2.2. Species Distribution Modeling

Predictive performance of the model as indicated by the area under the curve of the receiver operating characteristic (AUC) had a mean value of 0.937 across the replicate runs, with a standard deviation of 0.020. Variable contributions in the final model are described in Table S2. Precipitation seasonality (Bio 15), temperature seasonality (Bio 4), slope, and precipitation of warmest quarter (Bio 18) represented the variables with model contributions > 10%, and where aspect contributed 9.9%. The results of our SDM (Fig. 4) suggest significant range expansion during the mid-Holocene. This historic range expansion is particularly evident north of modern populations, paired with the apparent retreat of modern southern

suitable habitats. Results of our SDM also highlight the severe reduction in suitable habitat under a business-as-usual-carbon emissions scenario. POP 8, situated within Big Hole National Battlefield, was the only sampled population anticipated to persist under future climatic conditions.

2.3. Stakeholder Analysis

Based on legislative history, budgetary prioritizations, and general interest, major stakeholders were identified and categorized (Fig. 5) as established by Eden & Ackermann (2011). Players in this analysis were defined as individuals or organizations that hold both significant interest and power in shaping the events of a situation. With consideration to this issue, the Bureau of Land Management (BLM), the National Park Service (NPS), and the US Forest Service (USFS) were considered major players. Based on evaluation of genetic data, in conjunction with SDM data (Fig. 4), the determination of the Upper Big Hole Valley (POP8) as critical for future species persistence elevated the potential role of NPS as a very significant player. Subjects in this analysis were considered to be individuals or organizations that hold high interest in conservation initiatives, but unlike players, have little to no authority in the situation (Fig. 5). In this case, non-governmental organizations (NGOs), the academic community, and private industry represented a few of the most significant subjects in the context of *P. lemhiensis* conservation. Crowds were designated as individuals or organizations that hold little to no authority and interest in the proceedings of policy issues. Within the framework of *P. lemhiensis* conservation, this was considered to be the human population settled across both Idaho and Montana. Finally, context setters were defined as organizations or individuals that are within the scope of power to significantly affect conservation management for *P. lemhiensis* but to have little interest in the process. The prerogative of such organizations to impact action is derived from monetary allocation. In this context, the US Department of the Interior and the US Department of Agriculture set agency priorities based on annual budgetary allocation and specified project appropriations, and were considered context setters (Fig. 5).

Discussion

Appropriate conservation management of *P. lemhiensis*, holistically, has presented a challenge for land managers, especially considering the unequal management practices already applied. Big Hole National Battlefield (POP8), which supports the largest known population of *P. lemhiensis* has applied monitoring procedures since 2009 (Rodhouse et al. 2018; Stucki et al. 2013). Further, the area has undergone controlled burns and spotted knapweed invasion removal. To date, this population is the only area known to have recently applied an active management strategy. Outside of NPS, the species has been monitored by USFS, BLM, the Montana Natural Heritage Program, and the Idaho Native Plant Society (BLM 2016; Brown & Proctor 2018; INPS 2020). Monitoring has elevated *P. lemhiensis* as a species of conservation concern (SCC) within USFS, and a Type 3 species within BLM, indicating that the species is moderately endangered. Irrespective of classifications, no direct action or mitigation strategy has been applied by BLM or USFS. Further, these evaluations are less formally structured and haphazardly timed, when compared to those conducted by NPS. The extent to which actions undertaken by NPS have worked to enhance the genetic integrity and diversity of the population within the Battleground is unknown. A firm

understanding of how preceding management strategies has impacted populations, negatively or positively, can guide future management in establishing priorities for population conservation and act as a foundation for conservation plan formulation.

3.1. Population genetic diversity and structure.

Genetic differentiation (F_{ST}) is an estimate that provides insight into the dynamics of population connectivity. Traditionally, F_{ST} values > 0.15 are considered to represent significant genetic differentiation (Frankham et al. 2002) but more contemporary research suggests that F_{ST} values ≥ 0.20 indicate insufficient gene flow between populations such that harmful effects of inbreeding could manifest within small populations (Lowe & Allendorf 2010). The largest degree of differentiation, valuing at $F_{ST} = 0.280$, elaborates on the relationship between POP1 and POP6. Given the extent of geographic separation, nearly 62 miles in lateral distance, the approximate 776 meters difference in elevation, and the Beaverhead Mountain Range between both populations, this resulting degree of differentiation is expected. Correlation between genetic differentiation and geographic distance is a well observed pattern (Bontrager & Angert 2018; Hou & Lou 2011). A N_m value of 1.266 between POP1 and POP6, however, indicates some degree of gene flow. This phenomenon was detected in equally distant populations; POP5 and POP6 ($F_{ST} = 0.254$) and POP6 and POP7 ($F_{ST} = 0.249$), as well as the relationship seen between POP1 and every other population (Table 3). While F_{ST} values were broadly consistent with the number of migrants per generation, such that populations with the largest degree of differentiation had a smaller number of migrants per generation, and vice versa, it is notable that all values of N_m remain above 1. Based on Wright (1931) and ensuing analyses, one migrant individual per local population per generation is considered sufficient to maintain gene flow and impede differentiation (Mills & Allendorf 1996). The extent to which some populations are isolated from one another despite the detected gene flow is likely an indicator of the presence of a larger ancestral population in recent geological time. This population is likely undistinguishable in our current analyses due to the recency of divergence of the section in which this species resides, and the genus more broadly (Blischak et al. 2020; Wessinger et al. 2016; Wolfe et al. 2006; Wolfe et al. 2021). This conclusion is compounded by the remarkably low inbreeding coefficient values seen across all eight populations. Five out of eight populations were found to have negative inbreeding coefficient values, indicating a departure from Hardy-Weinberg equilibrium and an excess of heterozygosity within populations (Johnson & Shaw 2015). This, together with the lack of a significant difference between H_O and H_S values, is suggestive of outbreeding and gene flow amongst populations. Fitness traits were not measured in this study and neither inbreeding nor outbreeding depression could be assessed. In comparison to F_{IS} values observed in other vulnerable species of *Penstemon* (Table 4), the values detected in this study do not raise immediate concerns that can be applied to conservation management practices. However, given the aforementioned degree of differentiation between populations, the existence of a large, ancestral population is a plausible explanation for the high amount of connectivity detected. While the effects of habitat fragmentation, both negative and positive, are well documented (Fahrig 2003; Fahrig 2017), the strength of the response detected is dependent on several

factors, one of which is time since fragmentation. This is particularly true for measures of F_{IS} where effects become more pronounced and identifiable as more generations elapse (Schlaepfer et al. 2018).

While we were unable to detect ancestral connectivity across all eight populations, the results of the PCA show similarity across ancestral composition between POP1, POP7, and POP8, despite geographic isolation and physical distance between populations. This connectivity is likely the result of population shifts in response to climatic changes across the landscape, a phenomenon that is common for plant species following post glaciation (Huntley & Webb 1989). Although massive ice sheets such as the Cordilleran existed significantly farther North than extant populations of *P. lemhiensis*, areas of Western Montana were covered by mountain glaciers throughout the late Pleistocene (Alden 1953; Locke 1990). Further, the areas where both POP1 and POP7 are currently found was once within the Missoula flood extent and within bounds of the Late Wisconsin ice sheet (Cerling et al. 1994). Thus, the possibility of post-glacial expansion into Northern territory is likely an explanation for ancestral connectivity detected by the PCA. The expansion of suitable habitat detected in the mid-Holocene stands to confirm the likelihood of ancestral connectivity (Fig. 4). Following the Last Glacial Maximum retreat, southern populations would expand north into suitable, open habitats (Hewitt, 2000), as is often seen in *Penstemon*, a genus notorious for expansion into niches opened by glacial retreat (Wolfe et al. 2006; Wolfe et al. 2021). Suitable habitat estimates through the Last Glacial Maximum (Fig. 4) showcase the likelihood of southern populations, which would migrate north with a shifting climate.

3.2. Stakeholder Analysis

In addition to an understanding of the genetic integrity of populations, this study aims to evaluate the stakeholders relevant to the conservation of *P. lemhiensis* in order to better understand the influence of different individuals and organizations in directing appropriate conservation policy in the present and future (Bryson 2018). The identified major stakeholders, as outlined in Fig. 4, have been categorized based on their respective interest and authority in conservation action. Authority is defined, in part according to Cox and Jacobson (1973) as the “aggregate of political resources available to an actor”, as well as according to Ackerman & Eden (2011) as having the “capability to influence the delivery” of policy decisions. Interest is defined as having a politically, socially, morally, or economically motivated stake in the outcome of a policy decision (Bryson et al. 2011). Stakeholders with the most authority and influence can be considered key stakeholders (Eckhard & Jankauskas 2018) and should be both considered and leveraged in any policy decision regarding *P. lemhiensis*. We recognize that the stakeholders identified in this paper are by no means an exhaustive list and that other groups or organizations close to the issue, particularly those within marginalized communities, may have been excluded (Reed et al. 2009). It is therefore our recommendation that moving forward, conservation efforts are cognizant of this and work to bridge any perceived information gaps.

3.2.1. Players

Any conservation intervention initiatives for *P. lemhiensis* must thoroughly consider standing land management policies as well as the organizations with the legal discretion to mandate those policies

(Koontz & Bodine 2008). The eight populations of *P. lemhiensis* fall collectively across the jurisdiction of three major land management agencies - the National Park Service, the US Forest Service, and the Bureau of Land Management (Fig. 5). Each agency draws its discretion from separate mandates that, in turn, subsequently affects the prioritization of conservation initiatives.

The Bureau of Land Management (BLM) is nested within the Department of the Interior and as mandated by the Federal Land Policy and Management Act (FLPMA) of 1976 (43 U.S.C. §§ 1701 et seq.) and the National Environmental Policy Act (NEPA) of 1969 (42 U.S.C. § 4321 et seq), balances both multiple use and sustained yield in its' land management approach. Multiple uses of BLM-managed land include recreation, grazing, timber harvesting, and watershed, wildlife, and fish habitat management, and other conservation practices. Additionally, BLM facilitates federal mineral resource management and energy resource leasing and management. The US Forest Service, under the Department of Agriculture, is similar to BLM in its multiple use approach to land management. Following the discretion of FLPMA, NEPA, and the National Forest Management Act (P.L. 94–588; 16 U.S.C. §§ 1600–1614), the Multiple Use Sustained Yield Act of 1960 (16 U.S.C. §§ 528–531), and adjacent legislation, follows a land management style analogous to BLM. The Forest Service similarly facilitates a mission in managing land under principles of sustained yield and multiple use. Mandated to preserve the delegated land, water, and wildlife, the Forest Service also administers recreational activities, livestock grazing, timber extraction, and the management of renewable resources. Under the guise of multiple-use land management priorities, conservation priorities are difficult to equitably coincide with factors such as commodity production (Robbins 2013).

The National Park Service (NPS), while also maintaining a dual-purpose mission, focuses on preservation and recreation, as mandated by the National Park Service Organic Act of 1916 (16 U.S.C. § 1), the Wilderness Act of 1964 (16 U.S.C. ch. 23 § 1131 *et seq*), and the Historic Preservation Act (54 U.S.C. 300101 *et seq.*). Land and resources managed by the NPS are offered a greater degree of protection than those by the Forest Service or BLM due to differences in management priorities (Congressional Research Service 2019).

While the aforementioned legislations guide land management planning and prioritization, agency authority affords a wide degree of discretion towards actual implementation (Stern & Mortimer 2009). Both BLM and the USFS are often faced with competing interests in consideration of a singular land management approach. NPS faces this issue as well in balancing between recreation and conservation, albeit to a lesser degree. Statutes authorizing agency action will influence the priority placed on *P. lemhiensis* conservation efforts by each respective agency.

Consolidated conservation efforts across different federal and state agencies will be reliant upon cooperation across these agencies. The Council on Environmental Quality, for instance, mandates such cooperation under NEPA in instances of shared projects or interests. However, agencies have reported challenges in executing interagency projects; notably issues regarding timely communication, variation across agency standards, and a lack of memoranda of understanding defining agency roles (Stern & Mortimer 2009). Concentrated efforts across the BLM, USFS, and NPS to collectively manage and

conserve populations of *P. lemhiensis* must first acknowledge historic roadblocks to cooperation and actively seek to mitigate them.

3.2.2. Subjects

Subjects in this analysis are classified as individuals or organizations that hold high interest in conservation initiatives but have little to no authority in the matter (Fig. 5). In this case, non-governmental organizations (NGOs), the academic community, and private industry represent a few of the most significant subjects in the context of *P. lemhiensis* conservation.

The academic community plays a critical role in contributing to the policy decisions of state and federal agencies actively approaching various issues (Clancy & Glied 2012), especially issues directly relevant to species conservation (Posner et al. 2016; Rose et al. 2019). This can be accomplished through academic-led research focusing on the genetic diversity of species in question, peer-reviewed publications, and public dissemination of objective information as it impacts species conservation (Fisher et al. 2020; Taft et al. 2020; Walsh et al. 2014). Academics also have a high interest, for a variety of reasons, in the formulation of conservation protocols (Evans & Cvitanovic 2018). Assuring that scientific research is interpreted appropriately and offering feedback on written policy in the form of public comments throughout the Administrative Procedure Act rulemaking process. The academic community does not, however, maintain the legal authority or power to influence decision-making directly, unless through litigation.

Non-governmental organizations (NGOs), specifically those focused on species conservation and environmental integrity, hold a high degree of interest in conservation initiatives broadly (Boiral & Heras-Saizarbitoria 2017), but also more specifically for *P. lemhiensis*. NGOs, such as the Montana Native Plant Society and the Idaho Native Plant Society, work to educate the public on environmental and conservation issues, as well ecological values, and provide the resources to tackle issues firsthand. Similar to the academic community, NGOs lack the legal authority to mandate state or federal conservation management of *P. lemhiensis*. NGOs, as well as the academic community, hold the ability to litigate on behalf of conservation issues or in response to the absence of agency action. *Norton v. Southern Utah Wilderness Alliance* (542 U.S. 55, 2004), as well as the preceding lower court cases stand as notable examples of the litigative capacity of NGOs in affecting agency actions.

In addition to organizations with a commitment to conservation initiatives, others carry contradictory interest as it can interfere with their own organizational goals. Most prominently, the agriculture industry in both Idaho and Montana, among other private industries, is highly interested in any potential conservation measures applied towards *P. lemhiensis* populations. Private organizations retain significant political influence and are themselves subject to governmental regulation (Rainey 1997). Conservation mandates enacted by either BLM, USFS, or NPS can directly affect the interests of private industries in the area, which in this case, is predominantly private landowners and the agricultural industry within these two states. Both Idaho *P. lemhiensis* populations occur on land allotted by BLM for grazing - POP7 occurs on the Perreau Creek allotment while POP6 occurs on the Muleshoe allotment

(Bureau of Land Management, 2020). While the Montana populations do not occur on land allotted for grazing directly, POP3 occurs within approximately 130 meters of the Vipond-Glendale grazing allotment and within a reasonable distance such conservation management of the population could impact the neighboring allotment. Grazing allotment places individuals at risk of herbivory and trampling, as well as habitat alteration more broadly (Elzinga 1997).

3.2.3. Crowd

In this analysis, the crowd is designated as individuals or organizations that hold little authority and interest in the proceedings of conservation initiatives for *P. lemhiensis* (Fig. 5). The general civilian population of both Idaho and Montana have little power over the actions of BLM, USFS, and NPS and broadly low interest in their day-to-day priorities. This standing is conditional, and thus is subject to change across individuals based on their unique interests (Boiral & Heras-Saizarbitoria 2017). The citizenry has the capability of reaching out to representatives and public organizations when they feel the agency is not doing their due diligence regarding land management practices and obligations. This is most evident through citizen engagement during the public comment period of the Administrative Procedure Act.

3.2.4. Context Setters

Context setters are individuals or organizations that are within the scope of power to significantly affect conservation management for *P. lemhiensis* but have little interest in the process (Fig. 5). The prerogative of organizations to impact action is often derived from monetary allocation. In this case, the US Department of the Interior and US Department of Agriculture set agency priorities based on the annual budget and specified project appropriations. For example, the US Department of the Interior's 2021 budget authorizes \$244.1 million for the purpose of conserving, protecting, and enhancing both listed and at-risk fish, wildlife, plants, and their habitats, a 1.71% increase compared to their Fiscal Year 2020 budget (US Department of the Interior 2020). Further, the US Department of the Interior increased their Fiscal Year 2021 budget for listed species recovery by 13.5% when compared to Fiscal Year 2020. The US Department of Agriculture, which allocates annual funding to the US Forest Service, increased their budget for the National Forest System by 2.4% from Fiscal Year 2020 to Fiscal Year 2021 (US Department of Agriculture 2020). This prioritizes the implementation of programs that work to increase the health and resilience of Forest Service land while simultaneously meeting multiple-use land mandates. While both the Department of Interior and Department of Agriculture have generally increased their annual budgets for each agency, it is notable that only the Department of Interior specifically addressed the conservation and protection of at-risk or listed plant species within its budget summary. This detail, while incidental, denotes the priority placed by each department unto conservation initiatives. Organizations within the 'Crowd' designation are not considered key stakeholders but should be monitored regardless because of the impact they may have on policy decisions (Reed et al. 2009).

3.3. Conservation Management

The long-term persistence of a species is dependent upon its genetic diversity, a factor responsible for species resilience to deterministic and stochastic events as well as overall fitness (Bouzat 2010; Frankham 2005). Based on the genetic statistics and population structure, it is not immediately evident that *P. lemhiensis* is threatened or lacking in genetic diversity (Table 2). However, the high degree of physical separation, and the relatively small-estimated population sizes, despite detection of gene flow, is indicative of ancestral connectivity via a larger population. As a case in point, POP1 and POP4, two of the smallest estimated populations and physically distant, are still observed to maintain gene flow between each other. The relative recency of fragmentation makes aspects such as differentiation, inbreeding, and restricted gene flow more difficult to observe in our analyses. The small population sizes seen in a majority of the populations included in this study can contribute to the aforementioned effects and, eventually, to extinction (Markert et al. 2010). It is therefore recommended that, in the future, particular populations be monitored for ecological and demographic threats, along with measurements of fitness assessed within each population such that deleterious effects of inbreeding may be better detected (Reed & Frankham, 2003).

The high degree of differentiation observed between certain populations supports the conservation of as many populations as possible (Gaudeul et al. 2000). Priority should be placed upon populations with the most diversity; POP7 and POP8, in this case, albeit small in comparison. Future suitable habitat range, estimated based on climate change projections under a high-carbon emission scenario, severely reduce suitable habitat for *P. lemhiensis* (Fig. 4) such that only POP8 will likely persist (Fig. 4). While we advocate for the broadscale preservation of all *P. lemhiensis* populations, priority could be placed on populations with a high likelihood of survival under a rapidly changing planet.

Following the framework established by Ottewell et al. (2015), populations that are less differentiated from one another and show a high degree of gene flow, that is corroborated by close geographic proximity, should be monitored and managed to reduce threats to the populations – POP2, POP3, and POP4 fall into this category. Given that inbreeding within populations may be more serious than currently detectable, seed migration between close populations may also be more feasible. Seed germination practices should be cognizant of cold treatment and growth hormone requirements (Ramstetter 1983; Shelly 1990).

Populations that are highly differentiated from one another should be approached more cautiously. Analogously, these populations should be monitored, and ecological threats reduced. However, translocation of individuals, seeds, or pollen should be avoided due to risks associated with outbreeding depression (Frankham et al. 2011; Ottewell et al. 2015). Rather, focus should be placed on germplasm conservation. This includes methodology such as *in situ* and *ex situ* seed and pollen conservation, *in vitro* cultures, and crytopreservation (Oseni et al. 2018; Paunescu 2009).

As indicated by the stakeholder analysis, the organizations with the most authority and interest in conservation management of *P. lemhiensis* are BLM, NPS, and USFS. Shifts in climate and subsequent suitable habitat for *P. lemhiensis* will likely result in only NPS-managed populations, but nevertheless,

inter-agency relationships should be developed and fostered. Given the benefits of inter-agency collaboration in conservation, it is thus paramount that all three agencies work collectively to conserve the species uniformly (Maier & Wirth 2018). A cooperation tactic that may be utilized across agencies is the Landscape Conservation Cooperatives (LCC). Established in 2009, LCCs are intended to streamline interagency cooperation through a formal collaborative framework (NASEM 2016). Conservation management strategies founded on shared priorities across formal jurisdictions would, theoretically, lead to more effective and successful management. However, despite well intentions, it has become clear that conservation management is still approached independently by agencies. The complex web of federal, state, and local statutes and jurisdiction curtails cooperation and presents institutional challenges, even through programs such as LCCs (NASEM 2016). It is our recommendation that LCCs not be abandoned but utilized and built upon to ensure interagency cooperation in developing management strategies for *P. lemhiensis* conservation. Notably, collaborative organizational capacity must be developed in order to succeed (Foster-Fishman et al. 2001). Through the use of gap analysis, disparity in infrastructure and individual agency needs can be identified and remedied through various policy tools. Further, a formal participatory process should be developed and fostered. Expanding beyond the eight populations included within this study, all known, historic, observations of *P. lemhiensis* broaden the scope of agency involvement from three agencies to twelve, as well as privately managed land. This, together with the stakeholders identified in this study, constructs a need for a strong participatory process. Collaboration between public and private entities is a powerful tool (Ansell & Gash 2008) that should be explored.

An interagency communication strategy that allows for engagement of federal, state, tribal, private, and non-governmental stakeholders can be beneficial (Kark et al. 2015) and ensure the longevity of conservation management initiatives. While isolated to the issue of *P. lemhiensis* conservation, successful cooperative conservation strategies hold the potential to advance the dynamics of how issues of conservation are approached and valued in this country.

Declarations

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Tables

Table 1
Demographic Information for *Penstemon Lemhiensis* populations

Population	Latitude	Longitude	Elevation (m)	Estimated Population Size
POP1	45.8893972	-113.95269	1396	20–30
POP2	45.331521	-112.9085	2162	1300
POP3	45.6839728	-112.87973	2236	300
POP4	45.244886	-112.94612	2108	25–50
POP5	45.7828779	-112.51077	2352	300
POP6	45.0351065	-113.56013	2171	30–60
POP7	45.098286	-113.97044	1587	30–50
POP8	45.652331	-113.64881	1953	3000

Table 2
Penstemon lemhiensis population diversity metrics

Population	N	A	H _O	H _S	F _{IS}	F _{IS} 99% CI
POP1	9	1036	0.095	0.098	0.013	[-0.02, 0.07]
POP2	8	1071	0.113	0.112	0.001	[-0.07, 0.04]
POP3	9	1076	0.111	0.11	-0.021	[-0.06, 0.03]
POP4	9	1116	0.116	0.115	-0.005	[-0.05, 0.04]
POP5	9	1051	0.112	0.106	-0.039	[-0.1, -0.01]
POP6	8	1014	0.093	0.091	-0.019	[-0.07, 0.03]
POP7	8	1134	0.134	0.129	-0.034	[-0.08, -0.02]
POP8	33	1314	0.114	0.118	0.032	[0.01, 0.05]
Population genetics statistics are as follows: Number of Individuals (N), Inbreeding Coefficient (F _{IS}), Observed Heterozygosity (H _O), Gene Diversity (H _S), Number of Alleles (A).						

Table 3
Genetic Differentiation and Number of Migrants per Generation

	POP1	POP2	POP3	POP4	POP5	POP6	POP7	POP8
POP1	-	0.218	0.207	0.210	0.226	0.280	0.212	0.123
POP2	1.730	-	0.101	0.025	0.152	0.194	0.188	0.131
POP3	1.892	4.524	-	0.095	0.111	0.239	0.171	0.107
POP4	1.862	18.880	4.760	-	0.138	0.171	0.179	0.124
POP5	1.707	2.820	4.018	3.158	-	0.254	0.222	0.132
POP6	1.266	2.014	1.573	2.413	1.464	-	0.249	0.183
POP7	1.852	2.158	2.546	2.292	1.830	1.486	-	0.156
POP8	3.506	3.277	4.114	3.495	3.267	2.208	2.846	-
Lower diagonal represents the number of migrants per generation and the upper diagonal represents F_{ST} values.								

Table 4
Inbreeding Coefficients for Penstemon Taxa

Taxa	Estimate Population Size	F_{IS}
<i>P. scariosus</i> var. <i>albifluvis</i>	12,215	0.23
<i>P. scariosus</i> var. <i>cyanomontanus</i>	N/A	0.20
<i>P. scariosus</i> var. <i>garrettii</i>	N/A	0.29
<i>P. scariosus</i> var. <i>scariosus</i>	N/A	0.37
<i>P. debilis</i>	4,000	0.23
<i>P. albomarginatus</i>	100,000-200,000	0.16
<i>P. caryi</i>	3,375	0.10
Rodríguez-Peña et al. 2018; Stone et al. 2019 Wolfe et al. 2014; Wolfe et al. 2016		

Figures

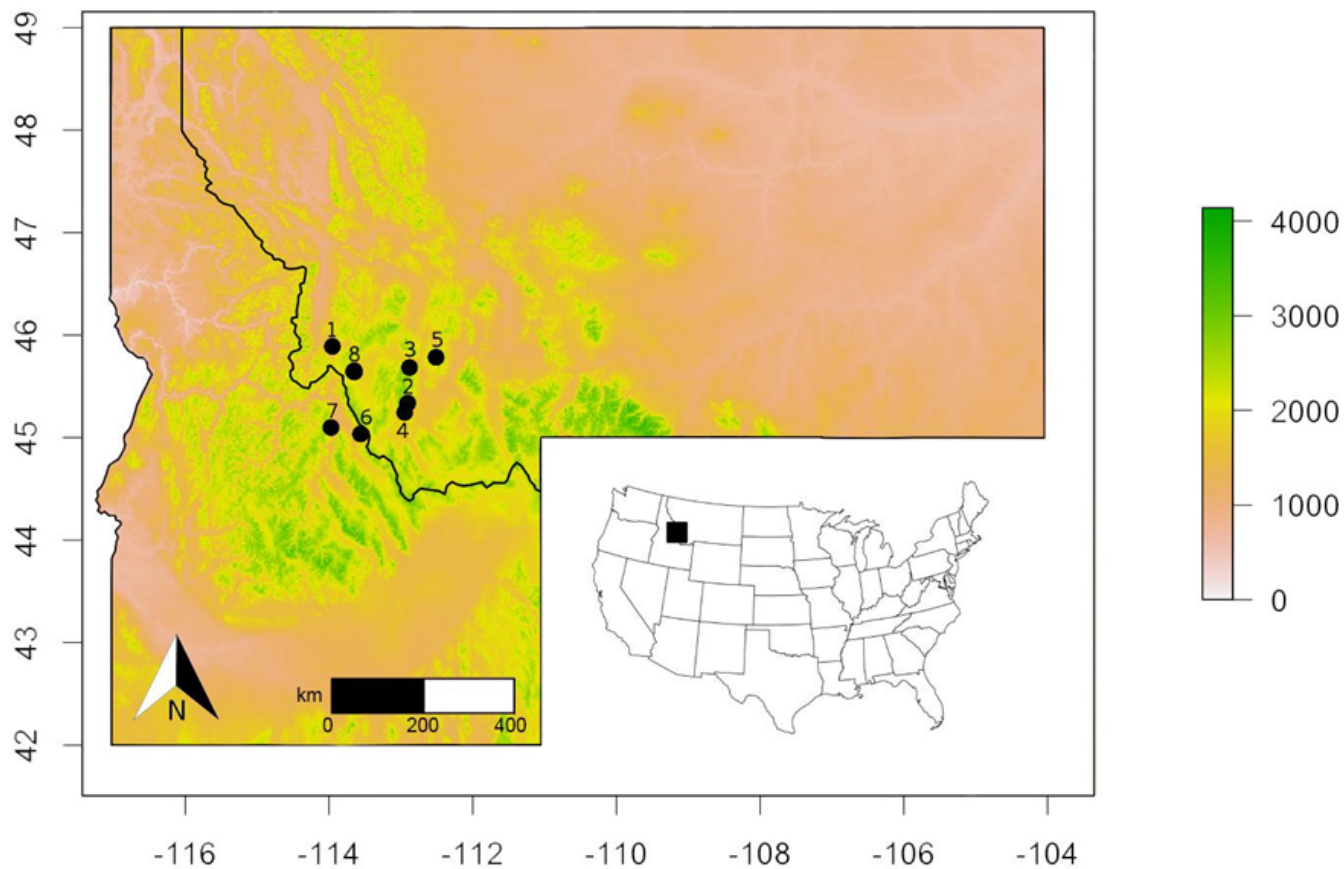


Figure 1

Elevation map with the distribution of *P. lemhiensis* populations used in this study. The legend on the right represents elevation in meters.

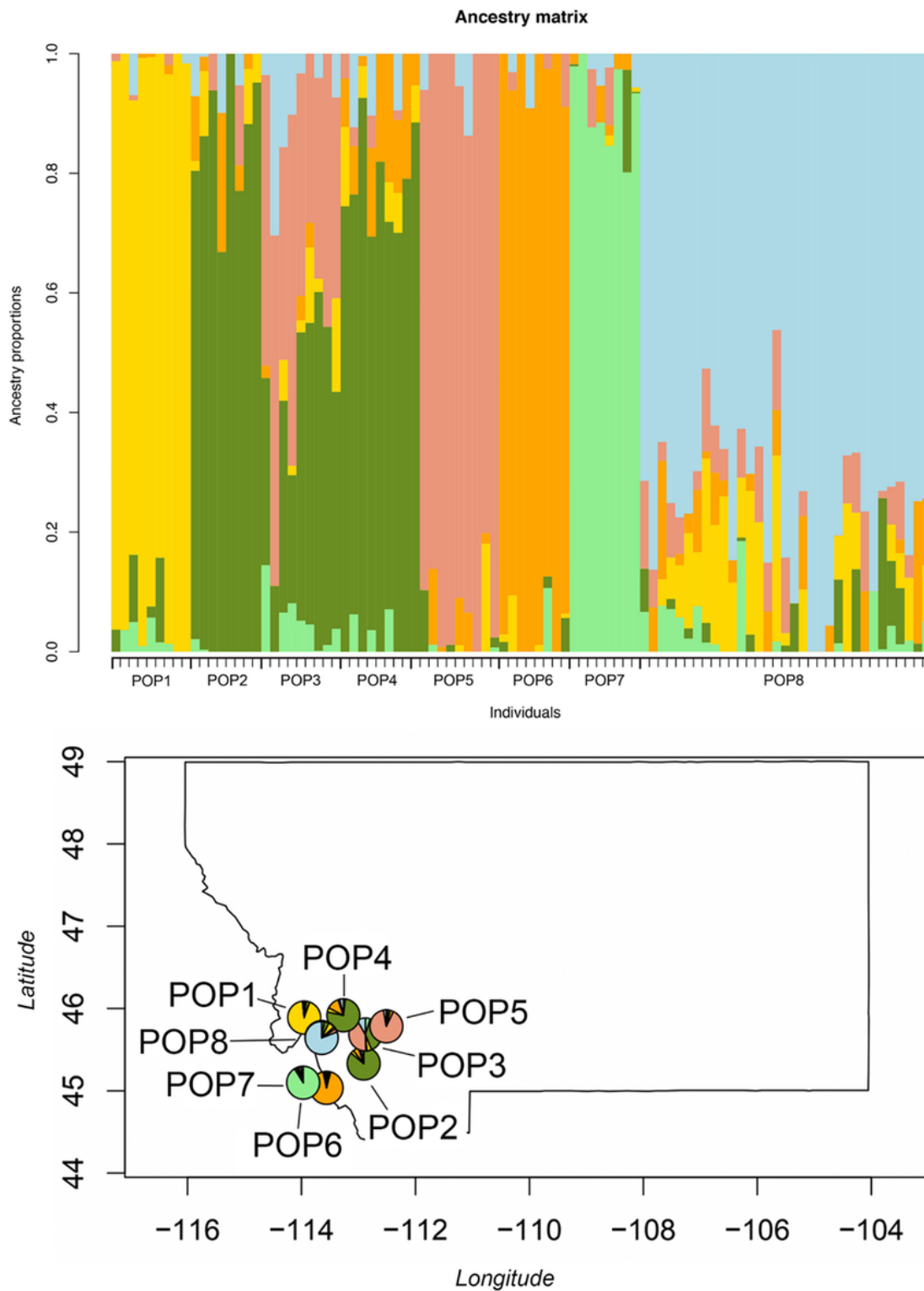


Figure 2

(TOP) Ancestry analysis of *P. lemhiensis*, $K = 6$. Populations labeled accordingly while each individual is represented by vertical bars. (BOTTOM) Map of the sampled population with pie charts representing population genetic structure based on the ancestry analysis of *P. lemhiensis* for the "best" value of $K = 6$. Admixture is present across all populations, but with higher degrees of genetic subdivision evident in geographically distant and isolated populations.

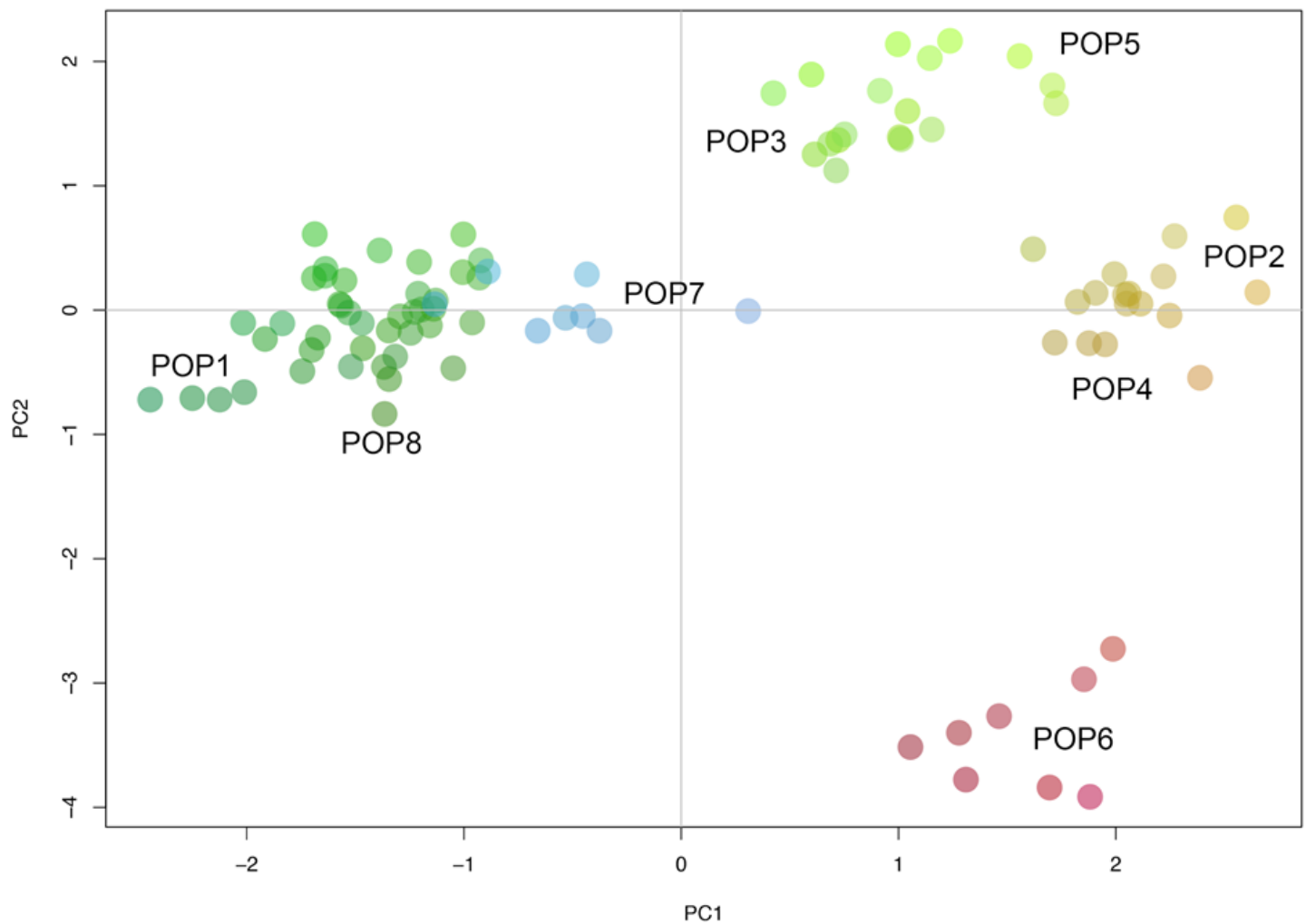


Figure 3

Principal Component Analysis of SNP data. Each dot represents one individual and is colored according to populations.

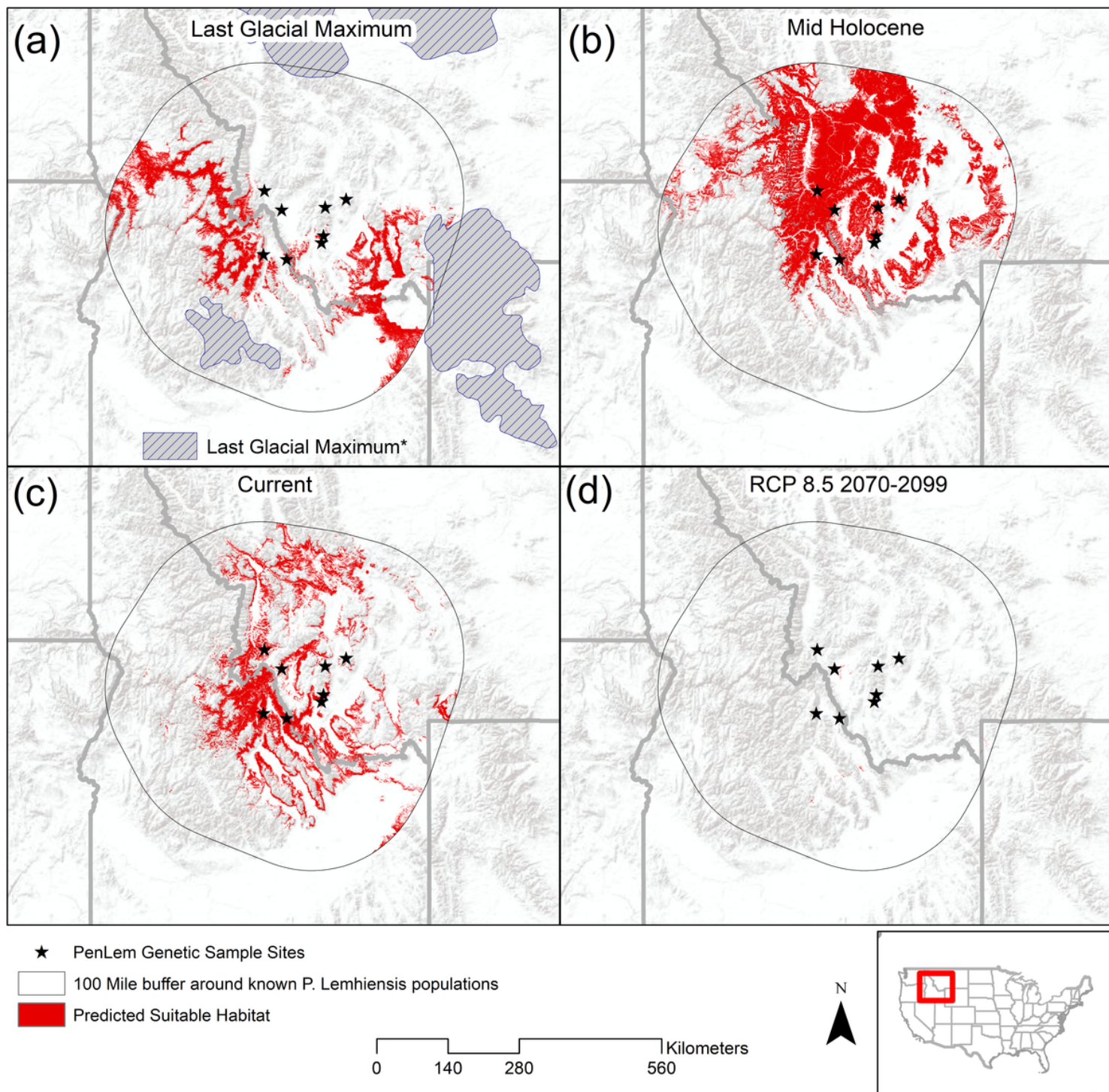


Figure 4

Species distribution models showcasing range estimations for *P. lemhiensis* based on climatic suitability across four periods: (a) the Last Glacial Maximum (0.020 Ma); (b) mid Holocene (0.0117 – 0 Ma); (c) current range; (d) future projects (2070-2099) based on representative concentration pathways (RCP) of 8.5. Range estimation is seen in orange.

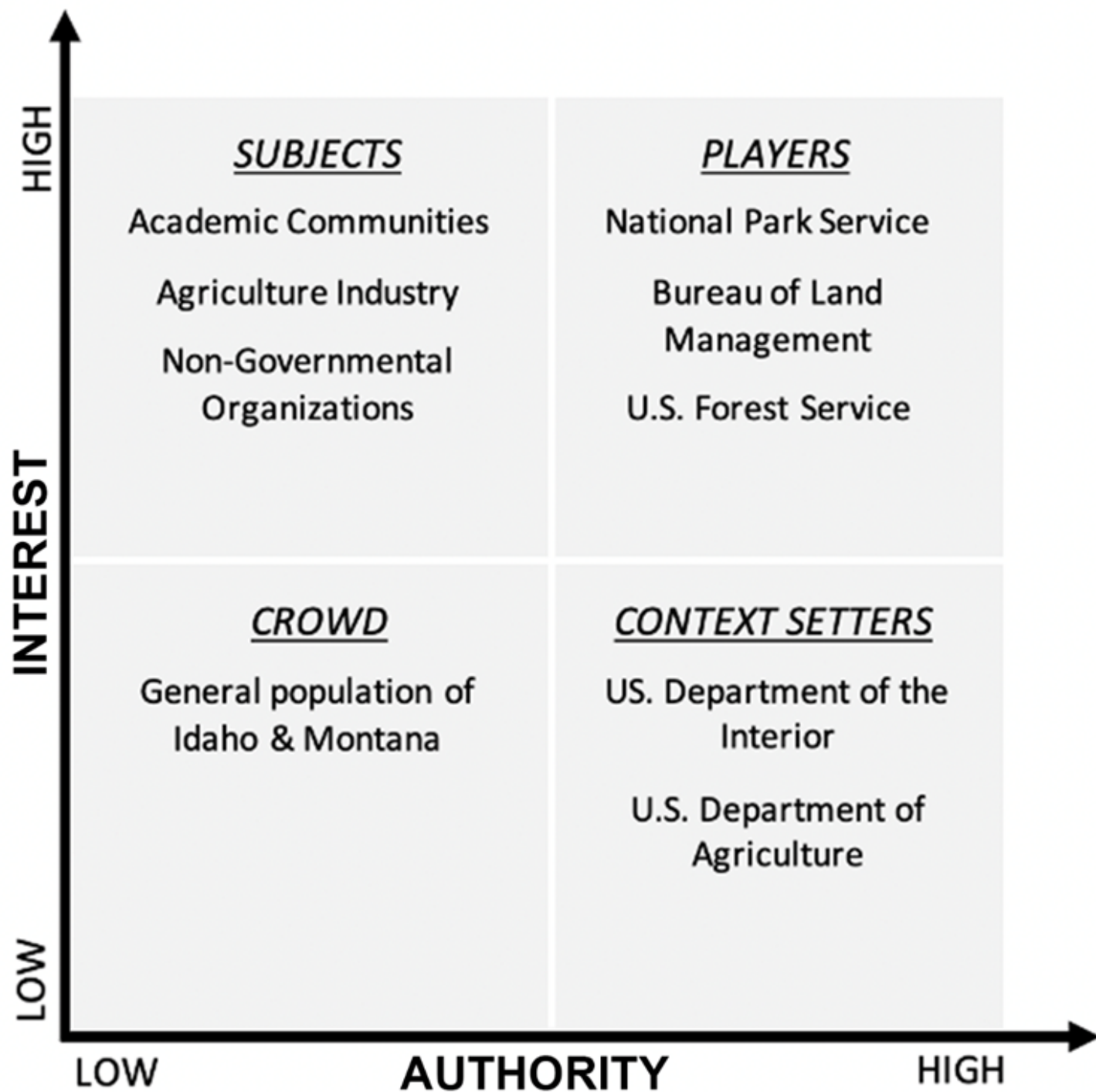


Figure 5

Authority & Interest Matrix as adapted from Eden & Ackermann (2011) framework. Prioritization should be placed on engagement with stakeholders that possess the highest interest and power in conservation management initiatives for *P. lemhiensis*.

Supplementary Files

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- [LemhiensisSupplementaryTablesandFigures.docx](#)