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Environmental Factors Driving Diversification of Ponderosa Pine in the Western United States

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Abstract: We used cluster analysis on 200-year-old tree-ring chronologies to examine the patterns that emerge from self-organization, driven by environmental heterogeneity, that might drive diversification in ponderosa pine (*Pinus ponderosa*). We determined the natural patterns on the landscape and then tested these groups against historically separated varieties within this species that could be evidence of diversification. We used 178 previously collected tree-ring chronologies from the western United States that were archived in the International Tree-Ring Databank. We explored a variety of clustering techniques, settling on Ward's clustering with Euclidian distance measures as the most reasonable clustering process. These techniques identified two (p = 0.005) to ten (p = 0.01) potential natural clusters in the ponderosa pine chronologies. No matter the number of clusters, we found that the ponderosa pine varieties *ponderosa* and *benthamiana* always cluster together. The variety *scopulorum* differentiates clearly on its own, but *brachyptera* is a mix of diverse groups, based on the environmental driving factors that control tree-ring chronology variability. Cluster analysis is a useful tool to examine natural grouping on the landscape using long-term tree-ring chronologies, enabling the researcher to examine the patterns of environmental heterogeneity that should lead to speciation. From this analysis, we suggest that the *brachyptera* variety should be more varied genetically.

Keywords: *benthamiana*; biogeography; *brachyptera*; cluster analysis; diversification; *Pinus ponderosa*; *scopulorum*; speciation; Ward's clustering

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1. Introduction

Diversification into varieties is the first step of speciation [1,2]. Environmental variables act together on a population to cause genetic drift [2]. Trees record the environmental variables that affect their growth, and, on broader scales, such as stand, watershed, and regional levels, these driving factors are usually controlled by climate [3–6]. Disturbance factors are another major forcing factor in the development and evolution of plants, where many pine species have adapted to fire and some have adapted to episodic insect outbreaks [7,8]. We can understand these factors that control diversification by examining the tree-ring record and comparing that to climate and disturbance factors. This deeper understanding of the driving factors behind tree growth can help us evaluate a species' vulnerability and aid us in conservation planning.

Ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) is widespread throughout the mountains of western North America [9,10]. Although the taxonomy of the species is a matter of some dispute, four geographically based varieties have been recognized: *P. ponderosa* var. *ponderosa* [North Plateau; Laws.], *P. ponderosa* var. *benthamiana* [Pacific; (Hartw.) Vasey], *P. ponderosa* var. *scopulorum* [Rocky Mountain; (Engelmann) E. Murray], and *P. ponderosa* var. *brachyptera* [Southwestern; (Engelm.) Lemmon] [10]. Emblematic of the western United States, ponderosa pine ecosystems also constitute one of the most important commercially logged forests in the western United States [11]. They are the habitat of countless animals and provide structure for other plants and insects. Their genetic diversity and classification have been studied for years with varying interpretations of what is a species, variety, or race within the population [12,13]. Potter et al. [13] used variants of the nad1 second intron mitochondrial deoxyribonucleic acid (mtDNA) minisatellite region to define two distinct haplotypes of Pacific (*P. p.* var. *ponderosa*) and Rocky Mountain (*P. p.* var. *scopulorum*) varieties of ponderosa pine, but they found little evidence for finer splits within these populations. Their results point to a need for a better understanding of the parameters driving diversification in this species. Willyard et al. [12] examined plastid clusters, using discriminant analysis of principal components, and suggested that the four historical varieties of *Pinus ponderosa* should be resurrected as unique species. Shinnerman et al. [14] mapped climatic niches and found that var. *ponderosa* favored areas with high winter precipitation, whereas var. *scopulorum* favored areas that had high summer precipitation.

Natural disturbances are one of the primary factors influencing landscape patterns and processes occurring across spatio-temporal scales [15]. They also represent opportunities to observe "evolution in action" [16]. In the montane and boreal needle-leaf forests of North America, fire and insect outbreaks constitute the dominant and most visible forms of natural disturbance [17,18]. These disturbances are influenced by factors occurring across a variety of spatial and temporal scales. For example, while regional climatic conditions can be an important influence on the likelihood of fire, local factors such as fuel loadings and topography are also important [19]. Temporally, a drought year that follows a wet period may produce different fire characteristics to one occurring after a period of moderate conditions. Disturbances can also interact across spatio-temporal patterns, resulting in a "nested hierarchy of space-time domains" [20]. Interactions between species, such as plants and their insect pathogens, are also thought to exhibit a hierarchical structure [21].

Research ecologists and forest managers alike have embraced the natural disturbance paradigm (e.g., [11,22]), which holds that natural disturbance is the primary agent of ecosystem change [23]. Accordingly, those disturbance factors influencing forest ecosystems over long periods and large areas (e.g., climate, fire, genetics, population biology, or past insect outbreaks) are of primary concern. In North American forests, insect outbreaks and fire constitute the most prevalent disturbances on the landscape, while the biogeographic history of species may be an important factor influencing and influenced by disturbances. Baseline data are necessary to provide a historical perspective of current forest conditions and enhance our understanding of the interaction between different processes [24,25]. In this respect, disturbance ecology has benefited from the environmental records of climate, fire, and insect outbreaks, provided by dendrochronology [8,19,26,27].

For example, recent mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks in western Canada and Colorado have been seven times larger in areal extent than any previously recorded outbreak [28]. The Pandora moth (*Coloradia pandora*) is an indigenous phytophagous insect whose larvae feed primarily on the foliage of ponderosa pine, although Jeffrey pine (*Pinus jeffreyi* Balf.) and lodgepole pine (*Pinus contorta* Douglas ex Louden) are alternate hosts [8,29–31]. Other incidental host tree species include sugar pine (*P. lambertiana* Dougl.) and Coulter pine (*P. coulteri* D. Don.) [32–35]. Pandora moth outbreaks have been documented throughout the western United States, mostly in Arizona, California, Colorado, New Mexico, Oregon, Nevada, Utah, and Wyoming [34]. Although the more northern distributions of ponderosa pine appear outside the historically mapped range of the Pandora moth, outbreaks have occurred in populations of each of the four varieties. By studying the history of ecosystem processes, we may determine their typical range of variation [36] and possibly identify the conditions that sustained or changed the system. These dynamics should be forcing speciation on the affected populations, as they are separated across the landscape and respond to different forcing factors. Master chronologies of stand-level tree-ring chronologies should reflect these forcing factors over the hundreds of years of the life of the trees and allow us to differentiate populations that are responding to different forcing factors.

Early work in population genetics underappreciated the influence that space and scale have on genetic variation within and among populations. This can be traced to Wright's [37] original description of hierarchical *F*-statistics to describe the genetic structures of populations. The model he described, of populations interacting via gene flow, was implicitly aspatial and dependent on the (arbitrary) assignment of individuals to populations. The arbitrary and non-spatial nature of genetic structure has been carried to more modern statistically well-developed measures and techniques, such as Nei's G_{ST} [38], Weir and Cockerham's [39] θ, and the analysis of molecular variance (AMOVA) [40]. Studies of genetic diversity that have examined scale usually are limited to fine-scale examinations within populations (e.g., [41,42]) or use different analytical techniques for the local vs. broad-scale analyses (e.g., [43]). In particular, while studies conducted on the local scale examine individuals, studies of diversification among populations (broad scale) use aggregate, population-level data. This aggregation of data makes these analyses subject to the modifiable areal unit problem (MAUP) [44,45].

Landscape genetics has recently emerged as a spatially and scale explicit research framework [12,13,46–48] for studying geographic patterns of diversification. In the landscape genetics paradigm, geo-referenced individuals, rather than populations, serve as the unit of analysis [46]. This eliminates the bias inherent when 'populations' are defined on the ground and enables one the ability to detect genetic discontinuities and barriers to gene flow that might otherwise go unnoticed [48]. Geo-referenced individuals also allow us the ability to analyze how the spatial scale of analysis is related to the amounts and patterns of diversification among populations, something that is impossible with population-level analyses that are not spatially explicit.

Piovesan et al. [49] used principal component and cluster analysis to identify geographical patterns in tree growth for 24 beech (*Fagus sylvatica*) tree-ring chronologies in Italy. Their purpose was to create bioclimatic zones and identify forest types from the analysis. We are taking this type of analysis one step further to examine the factors that mutually affect tree-ring widths through time and likely drive diversification of species in the ponderosa pine forests of the western United States. By using cluster analysis to enable populations to self-organize based on their site-level tree-ring chronologies, we can examine the emergent patterns to observe landscape scale processes.

In the subsequent analysis, we describe the specific spatial scale tendencies of the ponderosa pine varieties in western North America. The ecological importance of ponderosa pines, coupled with the abundance of reliable tree-ring records for this species, provide motivation for seeking insight into the genetic diversity of this particular species. Our analysis provides a novel approach for formally grouping tree-ring chronologies, based on how similar their ring widths behave over time. The tactic we employ through clustering finds natural groupings, which exist within the chronologies, instead of specifying the number of groups to be formed. This enables us to explore the natural patterns rather than imposing pre-defined patterns or scales of observation onto the studied subjects. It is expected that records from proximate geographical locations should be similar, since they will experience similar growing conditions. However, we hypothesize that records from groups of trees that are genetically diverse, perhaps from differing varieties of the species, would be grouped separately. We compare our results with the historical geography of varieties mapped by United States Geological Survey (USGS) [10], based on maps produced by EL Little, and discuss observed disparities.

2. Materials and Methods

A total of 217 stand-level tree-ring chronologies for the ponderosa pine species were available in the International Tree-Ring Databank (ITRDB). We downloaded the chronologies and checked them for accurate cross-dating using the program COFECHA (version 6.06p) [50]. Typical data cleaning, such as the removal of low correlating segments, chronologies with low sample depth, chronologies that were from sources other than ring width (such as maximum latewood density), and records with low series intercorrelation was performed, leaving 190 chronologies [6,51]. Our analysis calculated distances between ring-width indices over the years 1800 to 1960. Thus, it was additionally necessary to remove any chronologies missing index measurement(s) between 1800 and 1960. There were 12 such records, resulting in the 178 ponderosa pine chronologies analyzed here.

The goal of this analysis was to group similar chronologies in order to examine the genetic diversity of the ponderosa pine species, spatially. Since classification is unsupervised, or the true groups are unknown, cluster analysis is a method typically chosen for such situations [52]. There are two popular approaches to cluster analysis: specifying the total number of clusters, as proposed by Forgy [53] in K-means clustering, and selecting the number of clusters based on sequential groupings, as in hierarchal agglomerative clustering [54]. This analysis presents the results of Ward's method in hierarchal agglomerative clustering.

In hierarchal clustering, Ward's method minimizes the total within-cluster variance at each step. At the initial step, each chronology constitutes its own cluster. We used the standardized tree-ring chronologies to determine the similarity between each chronology and develop the naturally occurring clusters. The first step looked for the smallest squared Euclidean distance between two chronologies and created a cluster from those. The subsequent steps combined other chronologies or previously created clusters of chronologies so that the smallest increase in the total within-cluster variance occurred. Since variance is a scaled version of squared Euclidean distance, it was most straightforward to also utilize the Euclidean distance as a metric when searching for the closest chronologies or clusters to consider combining within the clustering algorithm.

A drawback associated with hierarchal clustering is that the technique does not directly recommend a final number of clusters. Hierarchal clustering algorithm results are typically displayed in a dendrogram, which shows the distance between objects combined and the created cluster for each step. The longer the distance between clusters, when combined, the greater the mismatch of the chronology information, and potentially more evidence of separate groupings. The bootstrap method proposed by [55] incorporates the idea that larger distances between groupings provide formal statistical evidence of different clusters. In their bootstrap algorithm, each step of the clustering procedure is associated with a bootstrap resampling process that creates a p-value for each branch of the dendrogram. At each branch, it is assumed in the null hypothesis that all chronologies within the branch are part of the same cluster. Small p-values are evidence that the branch should be split into two clusters. Thus, the procedure performs a sequence of hypothesis tests which may be used to formally select the number of clusters within the hierarchal clustering framework, instead of relying on a qualitative guess at the number of clusters that the simple elbow method provides [56]. The pvclust package [57] within R v. 3.6.1 [58] was used, with the ponderosa pine chronology data, to create bootstrap p-values for each branch. Our bootstrap approach was also more flexible than most traditional model-based clustering, which would require assuming that the underlying population distribution for ring-width indices had a named distribution, often Gaussian [59].

The presented significance level results are much more conservative than the typical 0.05 level. This choice was made due to a limitation of the bootstrap methodology. The bootstrap resamples were generated by creating a simple random sample with replacement of the record ring widths. Although the algorithm preserves the yearly dependence across records, it operates under the assumption that ring widths within records are independent. This is likely not true, and to combat the tendency of positively correlated observations to produce smaller p-values, the selected significance levels for the analysis were drastically reduced from 0.05.

3. Results

The chronologies self-organize into two ($\alpha = 0.005$) to ten ($\alpha = 0.01$) groups, according to the dendrograms associated with hierarchal agglomerative clustering, using Ward's method to select clusters and the Euclidean distance metric (Figure 1). When split into two groups, they roughly divide along the 37° N latitude line (Figure 2). Comparing these groupings to the varieties depicted by USGS ([10]; based on EL Little's maps), we can see that the records on the west side of the Rocky Mountains (1: var. *ponderosa* and 4: var. *benthamiana*) do not seem to be separable with this method. Many chronologies in the region associated with 2: var. *scopulorum* are classified into the same grouping. The southern regions, 3: var. *brachyptera* and 5 and 6: var. *arizonica* and *stormiae*, contain records that are a part of the remaining eight groupings, when $\alpha = 0.01$.

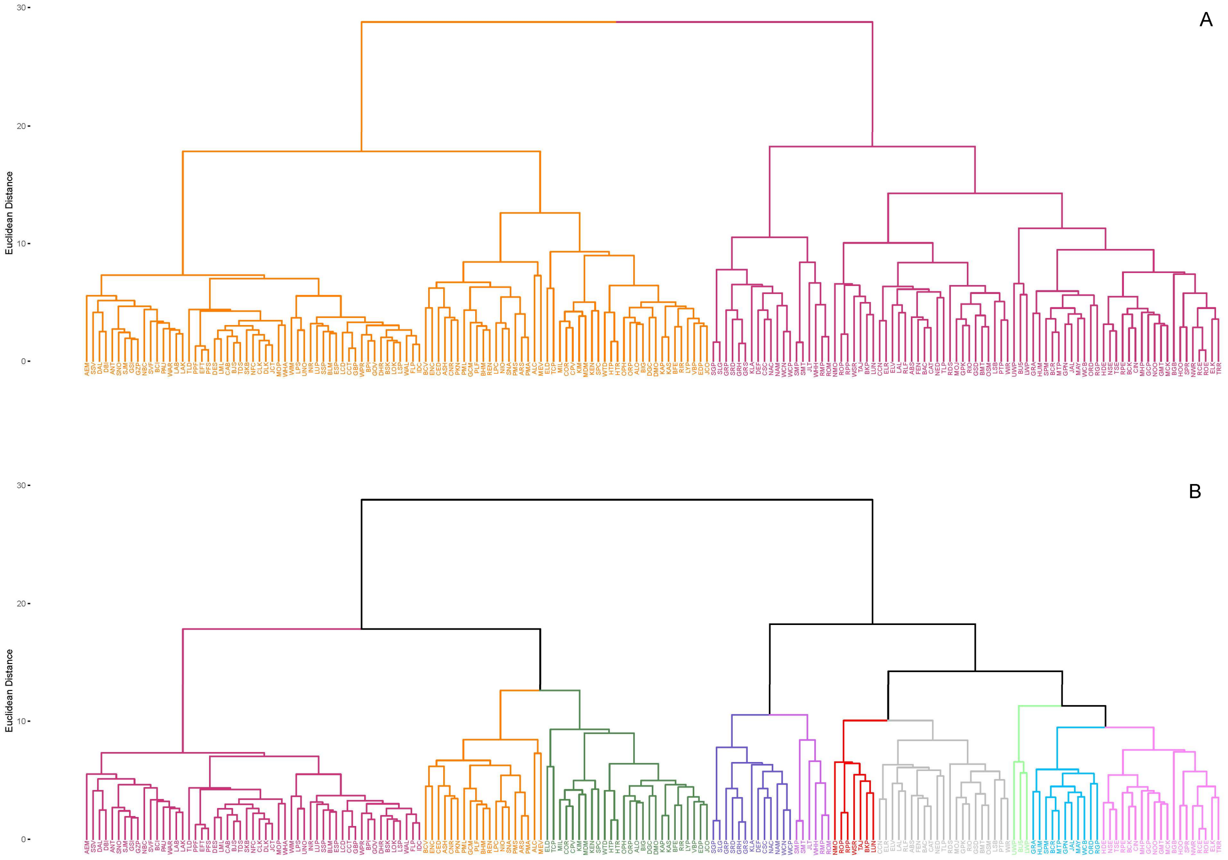

Figure 1. Dendrogram results from hierarchal agglomerative clustering with Ward's method to select clusters and the Euclidean distance metric. (**A**) Two clusters selected by bootstrap when $\alpha = 0.005$ (p-value of approximately 0). (**B**) Ten clusters selected by bootstrap when $\alpha = 0.01$ (p-value = 0.0075). The colors are arbitrary, but they match the mapped distributions in Figure 2.

As stated in the introduction, the taxonomy of the species is debatable, but there are currently four widely accepted varieties of the ponderosa pine species. Moreover, the dendrogram in Figure 1 visually seems to support four to five groupings within these chronologies. With the uncertainty associated with which significance level is appropriate to utilize with the bootstrap analysis, due to dependence within these data, we also provide the geographic results associated with three, four, and five clusters (all with p-values of approximately 0.0074) in Figure 3. With three clusters, we have a similar situation as in Figure 2A, where geographic regions 1, 4, and 2 are not differentiated. Increasing to four or five clusters does provide a grouping of records, mostly within region 2, and a grouping of records in regions 1 and 4. Region 3 combines many clusters that still have some spatial patterns, which might represent microclimatic and elevational differences.

Figure 2. Maps associated with bootstrap *p*-value size from hierarchal agglomerative clustering using Ward's method to select clusters and the Euclidean distance metric. Region 1 is var. *ponderosa*, region 2 is var. *scopulorum*, region 3 is var. *brachyptera*, region 4 is var. *benthamiana*, and 5 and 6 are var. *arizonica* and *stormiae* (USDA 1999). (**A**) Two significant clusters at alpha = 0.005 (*p*-value of approximately 0). (**B**) Ten significant clusters at alpha = 0.01 (*p*-value = 0.0075). The colors in the chart match the colors in the cluster analysis from Figure 1.

Figure 3. Maps associated with bootstrap *p*-value size from hierarchal agglomerative clustering, using Ward's method to select clusters and the Euclidean distance metric. Region 1 is var. *ponderosa*,

region 2 is var. *scopulorum*, region 3 is var. *brachyptera*, region 4 is var. *benthamiana*, and 5 and 6 are var. *arizonica* and *stormiae* (USDA 1999) [10]. (**A**) Forcing 3 clusters. (**B**) Forcing 4 clusters. (**C**) Forcing 5 clusters (*p*-values = 0.0074 for all clusters). The colors in the chart match the colors in the cluster analysis from Figure 1.

4. Discussion

The northern varieties (regions 1, 2, and 4 from USGS [10] and Critchfield and Little's work [9]) seem to be well separated from the southern varieties (regions 3, 5, and 6) based on the climatic and ecological forcing of the master tree-ring chronologies. They readily break into separate groups along the region 2–3 boundary, except for a small cluster of trees in northeastern New Mexico and southeastern Colorado (Figure 2A). Chronologies from regions 1 and 4 never separate, whether we force three, four, five, or even ten groups in the cluster analysis. Regions 1 and 2 remain distinct throughout the analysis, except for two outlier chronologies in region 2. However, region 3 contains a mix of groups that suggest that this region is more complex in environmental conditions controlling master chronology formation and might have a complex genetic signal. Regions 5 and 6, which are often identified as fully different species of *Pinus arizonica*, map onto chronologies from region 3. This could be from the strong monsoon influence in southern Arizona and northern Mexico.

Pinus ponderosa var *ponderosa* (North Plateau Ponderosa Pine) is traditionally mapped as a unique genetic group, but, in all of our analyses, it combines with what is identified as *Pinus ponderosa* var *benthamiana* (Pacific Ponderosa Pine). *Pinus ponderosa* var *scopulorum* (Rocky Mountains Ponderosa Pine) seems to be the clearest distinction, based on environmental forcing factors. It stands alone in every analysis above two basic units. Finally, we expected *Pinus ponderosa* var *brachyptera* (Southwestern Ponderosa Pine) to tell a more complex genetic story, as environmental factors easily split this group into many different subunits. This supports the findings by Williard et al. [13], who found three distinct haplotypes in this region. The tree-ring chronologies that represent two hundred years of growth in our analysis demonstrate the different environmental forcing factors that could be driving this diversification. Despite distinct environmental units that we have mapped using cluster analysis, the genetic pattern of haplotypes can be affected by the widespread disbursal of pollen, although the use of mitochondrial DNA, which is inherited from the mother cells, limits this homogenization. Complex environmental conditions in the Four Corners region may also play a role in creating smaller clusters of environmental drivers.

The patterns we observe make sense, with the Pacific Northwest clustered with northern California because of their similar moist maritime climate, suggesting that researchers should find genetic similarity between the varieties *ponderosa* and *benthamiana*. The variety *scopulorum* maps out as a distinctive group in almost all of our clusters. This suggests that the dry northern Midwest region (with minimal influence from monsoon rains) creates a distinctive habitat for ponderosa pine. Region 3, with the variety *brachyptera*, is the most heterogeneous cluster which matches the landscape. This region is topographically diverse, which creates feedback with climate and fire effects. This region also has a gradient of monsoon precipitation effects, with more seasonal rain in the southern portion of the region and less monsoon precipitation in the northern portion of the region. This heterogeneity creates a complex landscape of slope, aspect, micro-climate, and fire. We hypothesize that the variety *brachyptera* is likely to have greater genetic diversity than the other groups. Pandora moth outbreaks are more heterogenous across the landscape and will affect individual populations of trees rather than the entire region in most outbreaks. It is possible that the frequency of outbreaks in an area could be a genetic driver, but it does not appear to be an organizing agent across entire regions.

There is not an obvious geographic pattern for the eight groups that break out in region 3, but this behavior may have an intuitive explanation. Perhaps the trees within this region are more genetically diverse than those in regions 1, 2, and 4, and we have captured that behavior. Extrapolating from the historical literature, there may be some support to this hypothesis. The regions mapped by Little in 1966 indicated six varieties of the ponderosa pine [10]. If these less prevalent, yet geographically proximate, varieties crossed, it is reasonable to expect more genetic diversity in this region. Another explanation could be that these particular chronologies are capturing changing climate behavior, producing more dissimilarities in the ring-width indices. A third explanation is that the significance level of 0.01 is too high, when coupled with the dependence within the chronologies.

Clearly, we made several methodological choices, which are associated with the results of our analysis. The results presented here are due to hierarchal agglomerative clustering which incorporated Ward's method for selecting clusters using the Euclidean distance metric. However, clustering results can change with different distance metrics and methods for selecting clusters within hierarchal clustering. Moreover, K-means clustering and hierarchal clustering produce different results. The Supplementary Materials includes outcomes from cluster analyses of these data using three different methods for selecting clusters and four different distance metrics in hierarchal clustering. Qualitatively, we did not see much change when using different distance metrics. However, the choice of method for selecting clusters did produce wildly different groupings. We chose to explore the results from Ward's method in-depth, since Ward's method did not create any single-chronology clusters. K-means was eliminated from consideration due to the subjectivity associated with forcing a certain number of groups and attempts to use statistical methods to select the number of clusters, which were inconsistent.

5. Conclusions

Although the bootstrap analysis has a serious limitation with respect to the dependence inherent to tree-ring chronologies, we do believe that the analysis has provided some additional insight to the results. There is no evidence of a significant difference between the chronologies associated with regions where *ponderosa* and *benthamiana* varieties are typically found. There is also evidence that chronologies in the Southwestern U.S. and Northern Mexico are seemingly diverse, with no clear geographic patterns to their diversity. We find that the use of cluster analysis on site-level tree-ring chronologies enables the sites to self-organize and demonstrate patterns that reflect overarching drivers of climate and disturbance patterns. We suggest that future studies use cluster analyses of tree-ring chronology to identify these underlying patterns on the landscape that can then be explored using genetic analysis.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land13091428/s1.

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