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# Microevolutionary Processes in a Foundation Tree Inform Macrosystem Patterns of Community Biodiversity and Structure

**Helen M. Bothwell [1,*], Arthur R. Keith [2], Hillary F. Cooper [2], Julia B. Hull [2], Lela V. Andrews [3], Christian Wehenkel [4], Kevin R. Hultine [5], Catherine A. Gehring [2], Samuel A. Cushman [6], Thomas G. Whitham [2] and Gerard J. Allan [2]**

[1] Warnell School of Forestry & Natural Resources, University of Georgia, 180 E Green St, Athens, GA 30602, USA
[2] Department of Biological Sciences, Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ 86011, USA; arthur.keith@nau.edu (A.R.K.); hfc5@nau.edu (H.F.C.); julia.hull@coconino.edu (J.B.H.); catherine.gehring@nau.edu (C.A.G.); thomas.whitham@nau.edu (T.G.W.); gery.allan@nau.edu (G.J.A.)
[3] Tecan Genomics, Inc., 900 Chesapeake Drive, Redwood City, CA 94063, USA; lelavioletandrews@gmail.com
[4] Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango 34120, Mexico; wehenkel@ujed.mx
[5] Department of Research, Conservation and Collections, Desert Botanical Garden, Phoenix, AZ 85008, USA; khultine@dbg.org
[6] Wildlife Conservation Research Unit, Department of Zoology, The Recanati-Kaplan Centre, University of Oxford, Oxon OX13 5QL, UK; sam.cushman@gmail.com
* Correspondence: helen.bothwell@uga.edu

**Abstract:** Despite an increased focus on multiscale relationships and interdisciplinary integration, few macroecological studies consider the contribution of genetic-based processes to landscape-scale patterns. We test the hypothesis that tree genetics, climate, and geography jointly drive continental-scale patterns of community structure, using genome-wide SNP data from a broadly distributed foundation tree species (*Populus fremontii* S. Watson) and two dependent communities (leaf-modifying arthropods and fungal endophytes) spanning southwestern North America. Four key findings emerged: (1) Tree genetic structure was a significant predictor for both communities; however, the strength of influence was both scale- and community-dependent. (2) Tree genetics was the primary driver for endophytes, explaining 17% of variation in continental-scale community structure, whereas (3) climate was the strongest predictor of arthropod structure (24%). (4) Power to detect tree genotype—community phenotype associations changed with scale of genetic organization, increasing from individuals to populations to ecotypes, emphasizing the need to consider nonstationarity (i.e., changes in the effects of factors on ecological processes across scales) when inferring macrosystem properties. Our findings highlight the role of foundation tree species as drivers of macroscale community structure and provide macrosystems ecology with a theoretical framework for linking fine- and intermediate-scale genetic processes to landscape-scale patterns. Management of the genetic diversity harbored within foundation species is a critical consideration for conserving and sustaining regional biodiversity.

**Keywords:** arthropods; biodiversity management; community genetics; ecotype; fungal endophytes; macrosystems ecology; multiscale; nonstationarity; *Populus fremontii*

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**Citation:** Bothwell, H.M.; Keith, A.R.; Cooper, H.F.; Hull, J.B.; Andrews, L.V.; Wehenkel, C.; Hultine, K.R.; Gehring, C.A.; Cushman, S.A.; Whitham, T.G.; et al. Microevolutionary Processes in a Foundation Tree Inform Macrosystem Patterns of Community Biodiversity and Structure. *Forests* **2023**, *14*, 943. https://doi.org/10.3390/f14050943

Academic Editor: Huang Zhang

Received: 25 March 2023
Revised: 19 April 2023
Accepted: 28 April 2023
Published: 3 May 2023

## 1. Introduction

Anthropogenic change is causing widespread impacts to nearly all life on Earth [1], including unprecedented loss of global forest biodiversity and precipitous declines in insect communities [2]. Macrosystems ecology, born of the need to address the increasingly global scale of modern ecological challenges, integrates diverse disciplines to predict how hierarchical interacting processes operating at local to continental scales influence the emergence of macroecological patterns [3]. Predicting macrosystem properties, like biodiversity and community stability, requires understanding the underlying factors that drive pattern-process relationships across scales [4–6], and is a pressing challenge for mitigating widespread biodiversity loss under rapid global change [7,8]. Despite the recent increased focus on multiscale and interdisciplinary integration [3,9,10], there are few studies linking genetic-based processes in foundation forest species to ecological patterns at large geographic scales [11].

Macrosystem properties are, in part, defined by evolutionary processes. At the scale of individuals, fine-scale processes (e.g., natural selection) influence the abundance and distribution of genetic variants across heterogeneous environments. At intermediate scales, population-level processes (e.g., dispersal, mating, and genetic drift) contribute to the evolution of differentially adapted populations interacting across a regional landscape matrix. At broad scales, metapopulation dynamics are influenced by global climate patterns (e.g., post-glacial migration, and isolation by environment), resulting in the emergence of continental-scale patterns of macroecological structure [12–14]. Research in the field of community genetics, which investigates the role of genetic-based interactions in the emergence of community and ecosystem properties, has the potential to advance macrosystems ecology by providing a theoretical framework for linking these fine- and intermediate-scale evolutionary processes to continental-scale patterns [15–20].

A critical question in macrosystems ecology is whether local pattern-process relationships can be scaled up to predict regional and continental-scale properties. A wealth of studies utilizing common garden experiments have confirmed the role of host plant genetics in predicting heritable community phenotypes, and this association has been particularly well-documented for foundation tree species [21–23]. Through their role in modulating ecosystem processes, forest trees create locally stable biotic environments that associated species rely on [19]. Tree genetic variation has been shown to account for 20%–70% of variation in biodiversity of soil microbial, arthropod, lichen, and understory plant communities [17,23–25]. Communities directly interact with a tree's phenotype (e.g., phytochemistry, architecture, and litter nutrient composition), which is expressed as a function of its genotype responding to its environment. As we move beyond the relatively homogeneous environment of a common garden, we would predict that the relative contribution of environmental variance versus genetic variance increases, such that at increasing geographic scales, associated increases in environmental heterogeneity will explain a greater proportion of the variation in a community phenotype. A number of previous studies suggest support for the prediction of decreasing genetic influence on communities with increasing geographic scale [26–28]. The positive correlation between plant genetic similarity and associated community similarity [29,30] has been described by the 'Genetic Similarity Rule' [31], whereby more similar plant genotypes are predicted to support more similar community phenotypes. For example, Bangert et al. [31] used AFLPs to quantify the association between tree cross type and arthropod community phenotype across *Populus fremontii*, *P. deltoides*, *P. angustifolia*, and backcross hybrids and found the strength of this relationship decreased as the scale of investigation increased from stands to river systems to a single ecoregion. We extend this work in geographic, genetic, and community scope, using genome-wide SNP data to test whether the community response to genetic variation within a single foundation tree species can be detected up to the continental scale of a macrosystem, and further explore the sensitivity of this relationship between two very different dependent communities—arthropods and fungi. Specifically, we ask: At what scale do tree genotype—community phenotype relationships become undetectable on the landscape? How far does the influence of tree genetics extend before signal becomes noise? And does the scale of genetic organization influence detection? Here, we explore these questions to better elucidate the role of foundation forest trees as drivers of macroecological patterns of community organization.

To understand macroscale community organization, we first must define the geographic and genetic scales at which communities interact with their abiotic and biotic environments, respectively (Figure 1). Macrosystems can be conceptualized as hierarchies, in which mechanistic interactions at lower levels influence cross-scale emergence of higher level properties, and conversely, higher levels exert constraints on interactions at lower levels [3]. In the context of forest communities, tree genetics exerts a bottom-up effect on the emergence of community organization at higher trophic levels, whereas broadscale climatic patterns have a top-down effect, constraining the available local and regional species pools. At a local geographic scale, climatic heterogeneity is limited, whereas variation among individual trees may be large. For example, genetic-based differences in defensive chemistry can result in highly differentiated communities found on susceptible versus resistant trees standing just a few meters apart [20]. As genetic scale increases from individuals to populations of trees within watersheds, we expect climate and geography to exert a stronger influence. For example, geographic isolation limits gene flow and dispersal across river systems [32], and photoperiod and climate-related selection pressures drive variation in bud-flush phenology across populations [33]. Thus, the emergence of dependent insect communities may be influenced by both climate and variation in genetic-based tree traits across populations. At a higher level still, ecoregions are defined as regions with similar climatic, biotic, and geophysical properties [34], and have been widely adopted for guiding scientific studies and ecosystem management by state, federal, and non-governmental agencies [35]. Ecoregions can serve as useful proxies for managing regional biodiversity when detailed metapopulation data is lacking; yet, how well ecoregions define organizational structure varies among community members. For example, plants and vertebrates typically align more strongly with ecoregional boundaries than do arthropods and fungi [36]. At the associated genetic scale of organization, ecotypes denote intraspecific species units that form under the combined influence of shared biotic and abiotic selection pressures [37,38]. Ecotypes are recognized as important units of local adaptation in forest trees [39–42], shrubs [43,44], grasses [45], insects [46], and fungi [47]. Finally, we use macrosystem here to refer to the entire geographic distribution of a foundation tree species, whose realized niche is determined by the range of suitable climatic and biotic constraints to which it is adapted, and in turn represents the maximum extent of the biotic environment investigated as a determinant of continental scale community organization. Identifying the abiotic and biotic processes that give rise to community composition and structure and determining how these factors differentially affect communities across geographic and genetic scales is critical to gaining a deeper understanding of macroscale biodiversity patterns [48].

Here, we investigate the role of a foundation tree species in structuring macroecological patterns of community organization. We first present a comprehensive assessment of the population genetic and phylogeographic structure of Fremont cottonwood (*Populus fremontii* S. Watson), a native riparian tree species that is the foundation for much biodiversity throughout southwestern North America. This builds upon previous population genetic studies by Cushman et al. [49] and Ikeda et al. [39], expanding geographic sampling to encompass the full species' range into southern California, northern Utah and south into México. The more extensive genetic dataset (8637 SNPs compared with 12 MSAT loci) also provides a much finer-resolution assessment of phylogenetic structure among cottonwood populations and ecotypes to serve as a resource for ongoing research in this system.

We then investigate the relative contributions of tree genetics, climate, and geography as predictors of macroscale community organization. Given previous work suggesting genetic effects decrease with increasing geographic scale [31], we predict that climate and geography will exert a relatively greater influence on macrosystem community organization, yet we hypothesize that genetic effects will still be detectable at this scale. We quantify these relationships for two distinct communities: leaf-modifying arthropods and twig fungal endophytes. Previous studies have demonstrated ample evidence that tree genetics explains heritable variation in community phenotypes (e.g., biodiversity, stability) using common gardens, yet no studies to date have investigated this relationship at the continental scale using genomic data. The community assemblages investigated in this study directly interact with plant tissues, cuing into phenological, morphological, physiological, and phytochemical variation, all of which are under genetic control in this system [50–54]. Leaf-modifying arthropods interact with leaves via gall formation, herbivory, and altering the physical structure of leaves (e.g., rolling/tying leaves to form protective enclosures); conversely, endophytes exist fully embedded within the host's cellular matrix. While some endophytic fungi can become pathogenic when hosts are stressed, the majority form neutral or beneficial associations with healthy plants. In exchange for carbon, endophytes may provide numerous benefits to their hosts, including protection against herbivorous pests and pathogens, increased abiotic stress tolerance (e.g., heat, salt, and drought), and enhanced productivity [55]. Given the more intimate association of fungal endophytes living within the host's tissue, we hypothesize that tree genotype will be a stronger predictor of community structure for endophytes than arthropods.

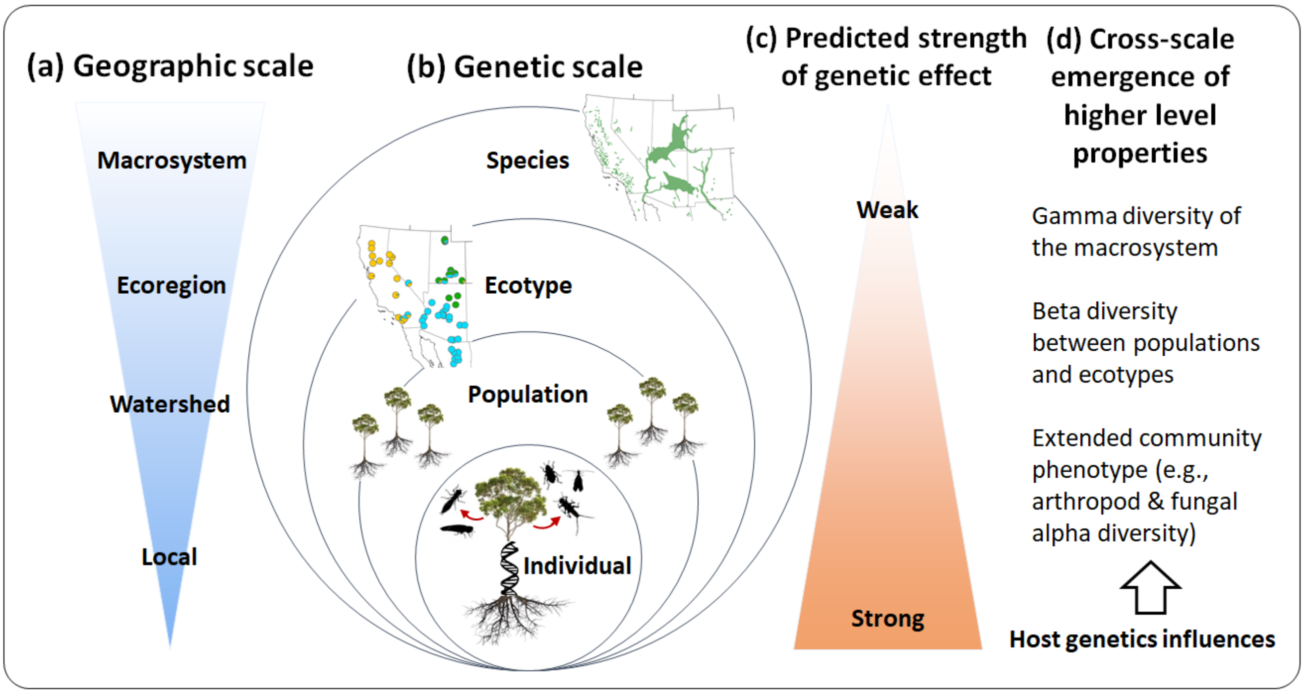

**Figure 1.** Conceptual schematic relating geographic and genetic scales of organization. (**a**) Environmental heterogeneity increases with geographic scale, from local stands to watersheds within ecoregions, to the entire macrosystem. (**b**) Within corresponding genetic scales of organization, we expect the (**c**) influence of host genetics on community phenotype to be strongest at the local level and diminish with increasing geographic scale. (**d**) Cross-scale emergence of higher-level properties (e.g., community composition and diversity) is then influenced by host tree genetic variation and structure.

We further ask whether the scale of genetic organization influences the ability to detect macroscale patterns of community structure. We test tree genotype—community phenotype associations considering the scale of individual trees, populations, and ecotypes, and hypothesize that the inferred strength of association will exhibit nonstationarity (i.e., changes in the effects of factors on ecological processes across scales [56]). The choice of scale is a critical component of macroecological analyses and may strongly impact conclusions. Accounting for nonstationarity by considering multiple scales of analysis has the potential to provide a more comprehensive understanding of the hierarchical, interacting processes typical of macrosystems, whereas investigating only a single scale introduces investigator bias and may be insufficient to detect or adequately characterize the true nature of pattern-process relationships. For example, Thompson and McGarigal [57] investigated habitat selection by bald eagles and found that the importance of individual habitat components (e.g., perch trees versus freedom from human disturbance) varied with the scale of analysis. Organisms utilize different habitat components at different spatial scales. We extend this concept to test whether associated communities are receptive to different genetic scales of their biotic habitat (host tree).

We address the following objectives and hypotheses. (1) We first assess population genetic and phylogeographic structure of *P. fremontii* ecotypes. We hypothesize that (2) Climate and geography exert a relatively greater influence on macrosystem community structure, however genetic effects are still detectable at the macroscale; (3) Tree genotype is a stronger predictor of community structure for endophytes than for arthropods; and (4) Tree genotype—community phenotype associations exhibit nonstationarity at the macrosystem scale (i.e., the scale of genetic analysis will influence the capacity to detect relationships). Tests of these hypotheses will help integrate community genetics theory with macrosystems ecology, providing an evolutionary basis for understanding macroscale patterns of community organization, and improving our capacity to support effective conservation policy and forest biodiversity management from local to continental scales [3].

## 2. Materials and Methods

### *2.1. Species & Collection Information*

Fremont cottonwood (*Populus fremontii* S. Watson) is a foundation riparian tree that occurs throughout the southwestern US and northwestern México. Previous research has identified three *P. fremontii* ecotypes within the US, based on population genetic structure and environmental niche differentiation [39,49]. We collected individually georeferenced leaf material from 453 trees at 58 sampling locations during the summer of 2014, stratified to maximize the geographic and climatic representation across the three major ecotypes (Table S1).

### *2.2. Tree Genotyping*

To assess population genetic structure within *P. fremontii*, we selected 5–6 trees per sampling location for genetic analysis. Leaf material was dried in Dri-Rite©, and ~0.2 g per sample was ground with a 2000 Geno/Grinder (SPEX, SamplePrep, Metuchen, NJ, USA). Genomic DNA was extracted with DNeasy 96 Plant Mini Kits (Qiagen, Valencia, CA, USA) and quantified using Quant-iT PicoGreen on a Synergy HTX Microplate Reader (BioTek Instruments, Inc., Winooski, VT, USA). The DNA was standardized to 5 ng/µL, and double digest restriction-associated DNA (ddRAD) libraries were prepared following a modified Peterson et al. [58] protocol. Briefly, 25 ng DNA was digested with MspI and EcoRI restriction endonucleases and ligated to double-stranded adapters in 20 µL reactions. Ligation products were amplified with indexed primers for 15 PCR cycles. Indexed ligation products were purified with PEG-8000 and Sera-Mag Speedbeads Carboxylate-Modified Particles (Thermo Scientific, Fremont, CA, USA; [59]). Indexed samples were pooled and size selected for 200–350 bp fragments using a Pippin Prep (Sage Science, Inc., Beverly, MA, USA). The fragment size distribution was assessed using Bioanalyzer high sensitivity DNA chips (Agilent Technologies, Santa Clara, CA, USA), and final DNA concentrations were quantified via qPCR (Eppendorf Mastercycler Realplex 4; Eppendorf, Inc., Westbury, NY, USA). The sequencing was performed on a MiSeq Desktop Sequencer (Illumina, Inc. San Diego, CA, USA) in 1 × 150 mode at Northern Arizona University's Environmental Genetics and Genomics Laboratory (Flagstaff, AZ, USA).

The quality filtering and variant calling of raw sequencing data used a modified Stacks v1.3 pipeline [60,61], with a minimum read depth of six and presence in at least three individuals required to call a locus. Using Bowtie [62], we removed reads that aligned to Huang et al.'s [63] *P. fremontii* chloroplast and Kersten et al.'s *P. tremula* × *P. alba* [64] mitochondrial reference genomes (NCBI accessions NC_024734.1 and NC_028329.1). The final dataset consisted of 322 *P. fremontii* genotypes, represented by 8637 loci filtered to one random SNP per locus.

### *2.3. Community Data Collection*

To quantify the relative contributions of tree genetics, climate, and geography in driving macroecological patterns of community organization, we sampled leaf-modifying arthropod and twig fungal endophyte communities on a subset of the trees collected above. Leaf-modifying arthropods (e.g., galling insects, leaf tiers, leaf rollers, and leaf miners) create distinctive, species-specific structures that conveniently allow for identifying species in their absence and reduce effects of temporal turnover when sampling across broad geographic regions [31]. Previous work by Cooper et al. [40] found that *P. fremontii* genotypes collected from southern Arizona to central Utah and grown in a common garden exhibited substantial variation in the timing of spring bud flush, spanning a range of 55 days. Conducting surveys from south to north from late May to early August allowed us to track these clines in host tree phenology, further minimizing temporal bias.

Arthropod surveys were standardized by branch diameter (2–3 branches/tree, ~35 mm total) to account for leaf area, and survey time (15 min/tree). Arthropod species were visually identified to the lowest possible taxonomic level; any unrecognized species were collected, later identified in the lab, and added to the Northern Arizona University Insect Collection. To assess twig fungal endophyte community structure, we collected 10 twigs/tree, including 3-years growth, directionally stratified around each tree's circumference. Twigs were frozen prior to genomic sequencing, and the variation in growth characteristics (number of leaves, leaf area, twig diameter, and twig length) was assessed among ecotypes.

### *2.4. Quantifying Fungal Endophyte Community Composition and Abundance using rDNA*

The total DNA was extracted from twig samples with DNeasy Plant Mini Kits (Qiagen). The fungal ITS2 rDNA was selectively amplified with 1µM fungal-specific primers 5.8SFun and ITS4Fun [65] using a Phusion Green Hotstart II High-Fidelity PCR Master Mix (Thermo Scientific). Amplification and indexing were performed following Alvarado et al. [66]. Libraries were pooled and sequenced on a MiSeq Desktop Sequencer in 2 × 300 mode.

Demultiplexing and quality filtering were performed with the split_libraries_fastq.py command in QIIME 1.9.1 [67] using a minimum quality threshold of q20 and 0 bad characters; only reads which satisfied these requirements for $\geq$95% of their length were retained. Chimeras were removed using the –uchime_ref option in VSEARCH 1.1.1 [68] against the UNITE chimera reference [69] for fungi. Sequences were de-replicated on the first 100 bases using QIIME's prefix/suffix OTU picker. The OTU picking was performed de novo with Swarm [70] at d4 resolution (~98.2% similarity). Taxonomic identities were assigned with BLAST in QIIME (maximum e-value = 0.001, 90% minimum sequence identity) against the dynamic UNITE database [71]. OTUs constituting < 0.005% of the total dataset were removed [72]. OTU tables were rarefied to the lowest sample depth for the purpose of assessing alpha diversity or normalized with cumulative sum scaling for all other analyses [73].

### *2.5. Population Genetic and Phylogeographic Structure of P. fremontii*

Genetic clustering was first assessed with principal component analysis (PCA) using SNPRelate [74] in R 4.0.2 [75]; three extreme outlier loci were identified and removed. We then applied the Bayesian clustering algorithm implemented in Structure 2.3.4 [76,77]. Assuming admixture and an independent alleles model, we ran 60,000 Markov Chain Monte Carlo (MCMC) generations with a 20,000 generation burn-in for $K = 1$–10 populations. Six iterations were run for each $K$. We identified the best-supported $K$ following the Evanno et al. [78] method ($\Delta K$ statistic) implemented in Structure Harvester [79], then used CLUMPP 1.1.2 [80] to merge replicate runs and generate a six-run consensus for the best-supported $K$. Results were visualized with Distruct 1.1 [81]. Phylogeographic structure and relatedness among *P. fremontii* sampling locations was estimated based on maximum-likelihood trees generated in PhyML 3.0 [82]. The Smart Model Selection (SMS) tool [83] coupled with Akaike's information criterion [84] was used to select molecular clock parameters for estimating divergence times. A General Time Reversible model was selected as the optimal nucleotide substitution model with gamma distributed rates across sites (GTR + Γ). Branch support was estimated based on 1000 bootstrap iterations.

### *2.6. Environmental Data*

We identified a suite of 20 environmental predictor variables that we hypothesize are related to gene flow and connectivity among *P. fremontii* and its associated communities ([49], Table S2). Wind is an important dispersal mechanism for cottonwood pollen and seed; therefore, we included average wind velocity vectors to test for the influence of directional resistance to prevailing spring (February-May) winds. Mean monthly wind data were derived from the NCEP North American Regional Reanalysis and averaged across 1979–1989 [85,86]. *Populus fremontii* is an obligate riparian species; gene flow is restricted by terrestrial uplands and low order streams, whereas mid-sized to larger, higher-order rivers facilitate gene flow in this species [49]. Thus, we included Böhner et al.'s [87] topographic wetness index (TWI) to account for the influence of hydrology on gene flow. This continuous hydrological metric incorporates both slope and upland drainage area in the steady-state wetness calculation (Table S2).

Cottonwood pollen dispersal and seedling establishment are also intimately linked to climate through its cueing of reproductive phenology and influence on the timing of spring flood events [40,88]. Cushman et al. [49] found that genetic differentiation increased with cumulative differences in winter and spring precipitation, and Ikeda et al. [39] linked differentiation among *P. fremontii* ecotypes to variation in minimum winter temperature and precipitation seasonality. We included nine bioclimatic variables representing temperature and precipitation means, minimums, maximums, and seasonality. Data represent 30-year averages (1970–2000, WorldClim v2, [89]). We predict that arthropod and endophyte communities are also strongly influenced by seasonal climate cues as their life cycles closely track phenology of resource availability in their hosts. For example, successful larval development requires alignment of hatch times with bud flush and leaf development, which vary by >55 days across *P. fremontii's* range [40]. Euclidean geographic and environmental distances were calculated using the ecodist R package [90].

### *2.7. Identifying Drivers of Community Similarity*

To understand the role of foundation forest trees in driving macroscale patterns of community organization, we assessed the relative contributions of tree genetics, geography, and environment using partial Mantel tests (999 permutations). We investigated these relationships at the genetic scales of individuals, populations, and ecotypes to determine how the scale of genetic organization influences the capacity to detect tree genotype—community phenotype relationships. Pairwise genetic distance among *P. fremontii* individuals was calculated using principal component analysis (PCA)-based genetic distance [32,91] on the first 15 PC axes, using SNPRelate and ecodist R packages [74,90]. The genetic differentiation ($F_{ST}$) among sampling locations (hereafter referred to as populations) was derived from Stacks [60]. Individual- and population-level community relatedness matrices were constructed using Bray-Curtis dissimilarity, incorporating both composition and abundance data [92]. The multi-response permutation procedure (MRPP) in PC-ORD was used to detect whether arthropod and fungal communities were significantly differentiated among ecotypes [93].

We next assessed the degree to which genetic differentiation in *P. fremontii* is correlated with climate. We used PCA to visualize genetic groups in climate space, followed by a permutational multivariate analysis of variance to test whether genetically defined groups exhibited significantly different climate niches (perMANOVA, 999 permutations, *adonis* function, vegan R package [94]). Because communities ultimately interact with host tree phenotypes, we assessed the variation in twig and leaf characteristics using non-metric multidimensional scaling (NMDS) in PC-ORD. NMDS is a nonparametric ordination method that is robust to non-normally distributed data [95]. NMDS was followed by an analysis of similarity (ANOSIM) to determine if functional traits segregating in ordination space were significantly differentiated among *P. fremontii* ecotypes. Lastly, we used redundancy analysis (RDA) to identify which environmental variables had the strongest influence on macroscale patterns of community organization. RDA is a multivariate constrained ordination analysis, an extension of multiple linear regression in which multiple explanatory variables (e.g., environmental predictors) are used to summarize variation in multiple response variables (e.g., community composition and abundance) [95].

## 3. Results

### *3.1. Population Genetic and Phylogeographic Structure of P. fremontii*

Our dataset including 8637 SNPs is largely in agreement with the pattern of genetic structure found by Cushman et al. [49], using 13 MSAT markers. Based on Cushman et al.'s [49] genetic groupings, Ikeda et al. [39] defined three *P. fremontii* ecotypes within the continental US, which occupy significantly different climate niches: the Sonoran Desert (SD), Central California Valley (CCV), and Utah High Plateau (UHP). We extended sampling efforts to include the full species' range, with additional sampling targeting southern California, northern Utah, and the Mexican states of Sonora and Durango. Interestingly, the more extensive collections did not reveal additional primary genetic structure; $K = 3$ remained the best supported number of populations (Figure 2). However, both PCA (Figure S1) and an additional $\Delta K$ peak at $K = 6$ indicate support for secondary hierarchical substructure. Therefore, we ran additional structure analyses within each of the three primary genetic groups, following the same methods as above. Hierarchical substructure analysis supports $K = 6$, with each of the three primary ecotypes further split in two (Figure S2). Based on these findings, we amend Ikeda et al.'s [39] ecotype designations to separate Southern California (SC) from the more northern CCV ecotype, split the SD ecotype into Northern Sonoran Desert (NSD) and Southern Sonoran Desert (SSD) ecotypes, and differentiate the Utah High Plateau (UHP) from the Southern Colorado Plateau (SCP; Figure 3). Phylogeographic structure among *P. fremontii* sampling locations further supports genetic divergence with strong branch support (95–100%) for the three primary ecotypes (Figure 4). Hierarchical substructure nests monophyletic groups by geography within the three major clades.

### *3.2. Identifying Drivers of Community Similarity*

We next quantified the relative contributions of tree genetics, climate, and geography in driving macroscale patterns of community structure. We investigate these relationships at the scale of individual trees, populations, and ecotypes to determine if scale of genetic organization influences capacity to detect these patterns. We predict that climate and geography exert a relatively greater influence on community organization at the scale of the macrosystem, yet we hypothesize that genetic effects are still detectable at this scale. We further hypothesize that tree genetics is a stronger driver of community structure for fungal endophytes compared to arthropods, and that tree genotype–community phenotype associations exhibit nonstationarity across different genetic scales of analysis.

For the fungal endophyte community, geographic and climatic distance contributed equally to community similarity across individual tree genotypes (Table 1, partial Mantel $r = 0.09$, $p = 0.07$, $p = 0.08$, respectively); however, these relationships are weak. In contrast to our hypothesis, we detected no independent effect of genetic distance. At the population scale, climate distance was no longer significant. Instead, genetic distance emerged as the primary driver, explaining 17% of variation in community similarity ($p = 0.04$), with a smaller contribution from geographic distance (15%, $p = 0.03$). However, reciprocal partial Mantel tests partitioning out the effects of genetic and geographic distance on each other were non-significant. Given this confounding result, we tested for isolation by distance (IBD). We detected a weak relationship between genetic and geographic distance among individual tree genotypes (Mantel $r = 0.095$, $p = 0.02$); however, IBD among populations was substantial (Mantel $r = 0.477$, $p = 0.001$).

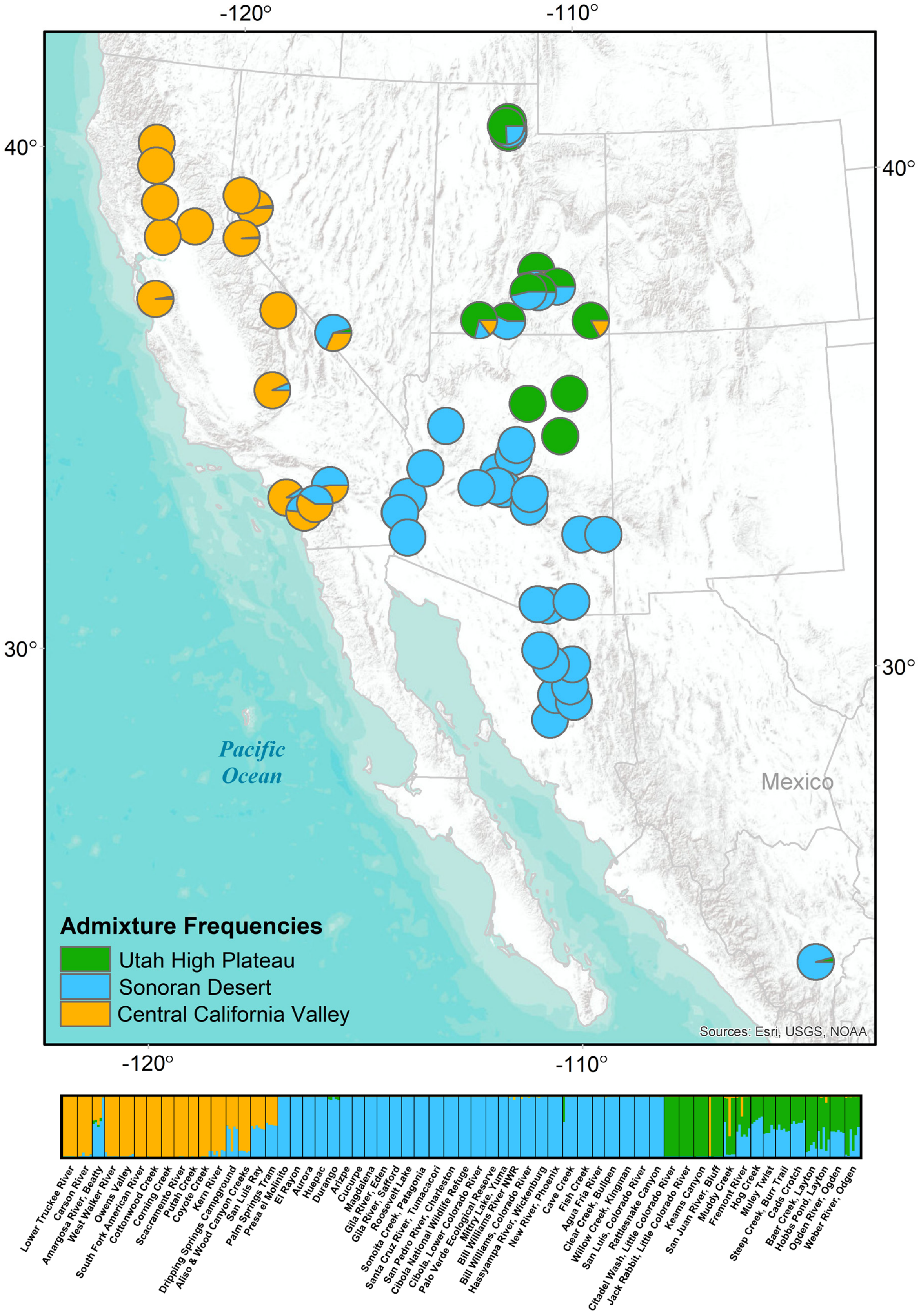

**Figure 2.** *Populus fremontii* segregates into three primary genetic lineages across its range. Different colored pies and bars in the Structure $q$ plot indicate admixture frequencies.

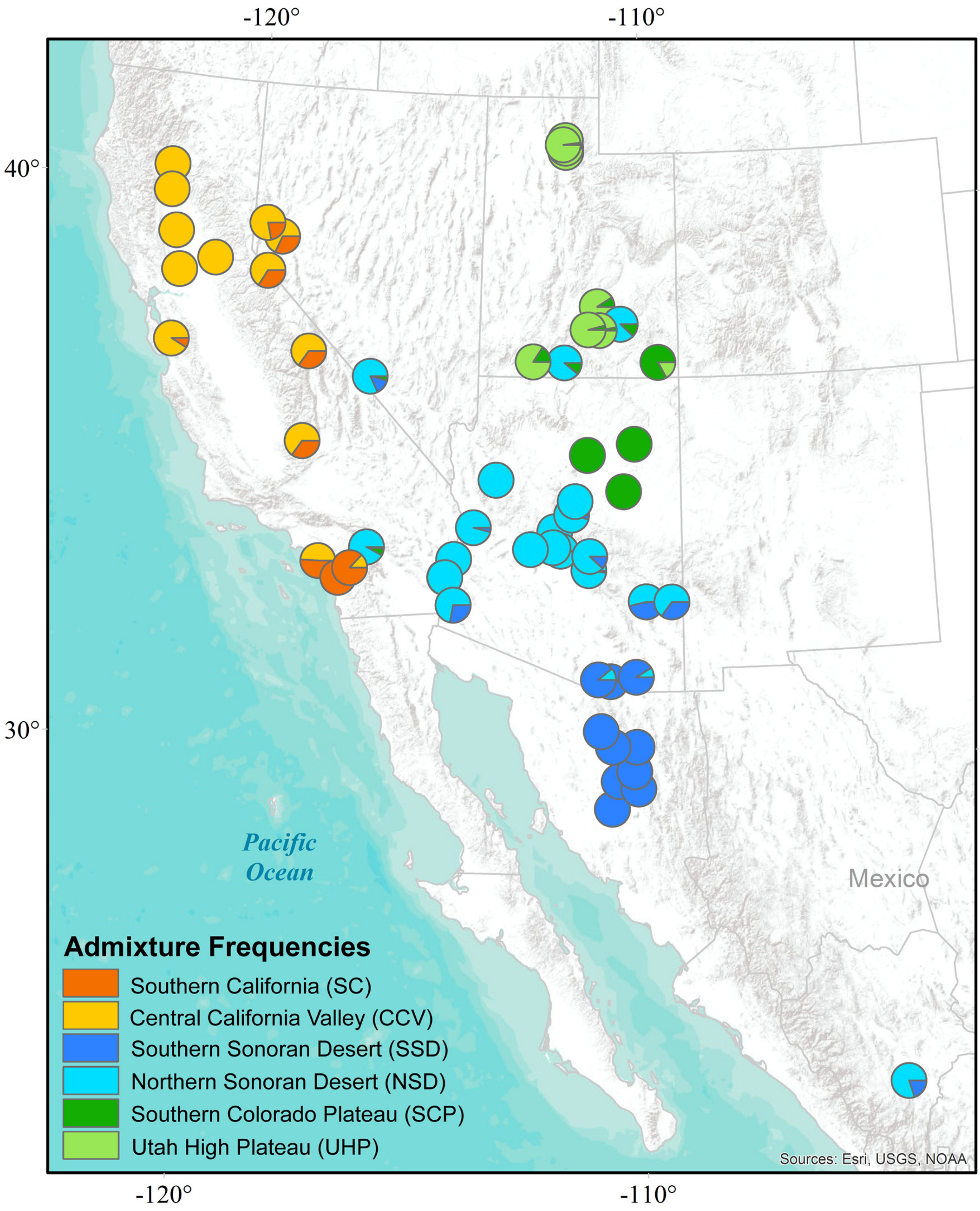

**Figure 3.** Admixture frequencies illustrate secondary hierarchical structure ($K = 6$) within the three primary ecotypes.

In agreement with our hypothesis, we found that climate distance was the primary driver of broad-scale arthropod community similarity, accounting for 17% ($p = 0.001$) of variation among individual trees after partialling out the effect of geographic distance.

No independent geographic effect was observed after accounting for climate distance. Supporting our hypothesis of nonstationarity, we found the strength of this association was amplified at the scale of populations, with climate independently explaining 24% ($p = 0.02$) of the variation in community similarity, and a smaller independent contribution detected for geography (Mantel $r = 0.15$, $p = 0.06$). At the individual tree scale, genetic distance was not significant (Mantel $r = -0.024$, $p = 0.66$). Conversely, host genetics explained 13% of community similarity among populations ($p = 0.06$), although this relationship is confounded with the effects of geography and climate.

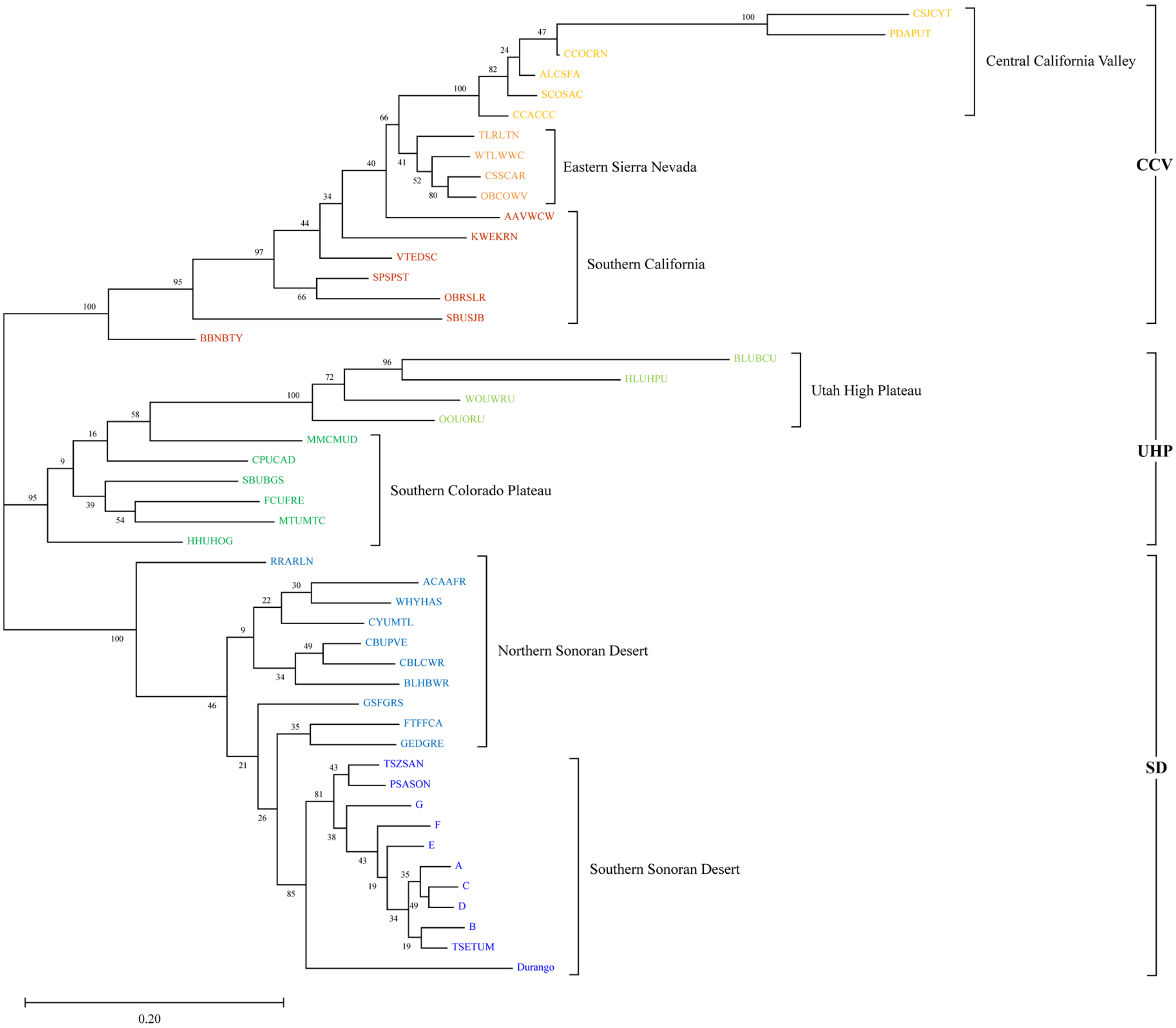

**Figure 4.** Phylogenetic relationships within *P. fremontii* show strong support for three monophyletic lineages, in agreement with the three primary ecotypes defined by [39]. Node values indicate bootstrap support. Substructure within the three primary ecotypes clusters by geography; lower bootstrap values within lineages are consistent with admixture results observed from Structure.

Supporting our hypothesis that tree genetic effects would extend to the scale of the macrosystem, tree genetic variation remained a detectable driver of community organization among ecotypes (Figure 5, NMDS stress scores: 0.19 for both communities, MRPP: $p < 0.0001$, $p = 0.04$, respectively), as did climate (Figure S3, RDA $R^2_{\mathrm{adj}} = 0.248$, $p = 0.001$); however, the variance partitioning of these components was not possible given near-singularity. For brevity, only results for $K = 3$ are presented here, however we found similarly strong community differentiation when considering the six ecotypes.

**Table 1.** Mantel *r* correlations quantifying the relative contribution of genetic (GenD), geographic (Geog), and climatic distance (Climate) in driving community similarity at the scale of (a) individual tree genotypes and (b) populations. Simple Mantel tests are represented along the diagonal. Remaining values represent partial Mantel tests, with the amount of variation in the associated community being explained by the column variable while partitioning out the effect of the row variable. For example, 9% of the variation in the endophyte community across individual tree genotypes can be explained by geographic distance after accounting for the effect of climate distance.

| **(a)** | | **ENDOPHYTES** | | | | **ARTHROPODS** | |
|---|---|---|---|---|---|---|---|
| | Geog | Climate | GenD | | Geog | Climate | GenD |
| Geog | 0.16 ** | 0.09 † | 0.07 | Geog | 0.08 ** | 0.17 *** | −0.03 |
| Climate | 0.09 † | 0.16 ** | 0.04 | Climate | −0.02 | 0.18 *** | −0.05 |
| GenD | 0.15 ** | 0.14 * | 0.09 | GenD | 0.08 ** | 0.19 *** | −0.02 |
| **(b)** | | | | | | | |
| | Geog | Climate | GenD | | Geog | Climate | GenD |
| Geog | 0.15 * | 0.01 | 0.10 | Geog | 0.44 *** | 0.24 * | −0.09 |
| Climate | 0.12 † | 0.09 | 0.16 † | Climate | 0.15 † | 0.47 *** | −0.16 |
| GenD | 0.05 | 0.07 | 0.17 * | GenD | 0.43 *** | 0.48 *** | 0.13 † |

$p < 0.1$ †; $p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***.

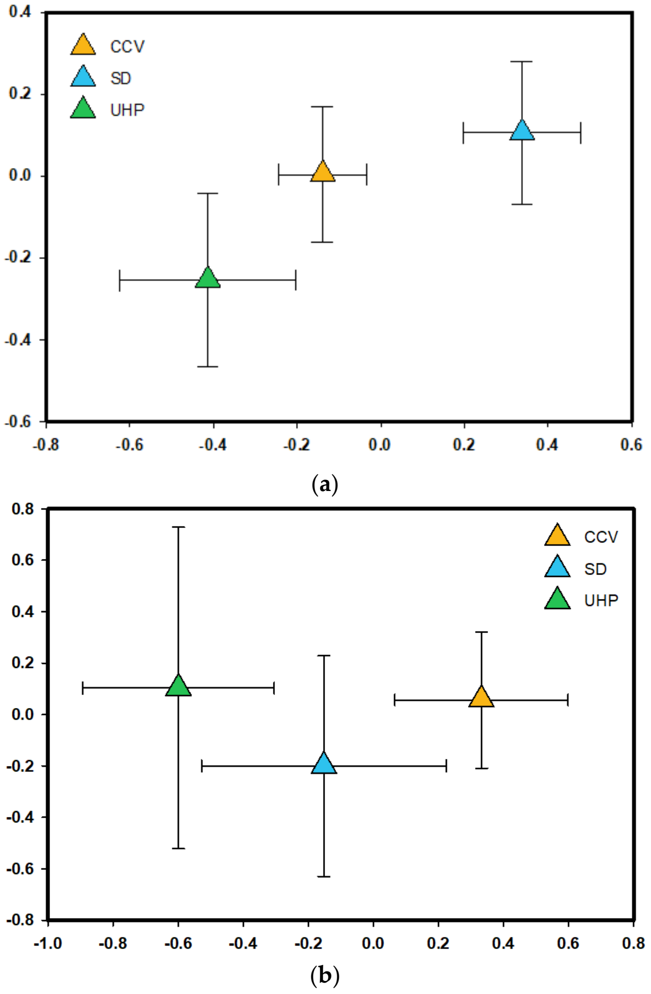

**Figure 5.** (**a**) Leaf-modifying arthropod and (**b**) twig fungal endophyte communities are significantly differentiated across ecotypes (MRPP, $p < 0.0001$, $p = 0.04$, respectively). Centroids represent community means for each ecotype; error bars indicate 95% confidence limits.

To better understand the degree to which *P. fremontii* genetic structure is correlated with climate, we assessed niche differentiation among ecotypes. We predicted that *P. fremontii* genetic structure is associated with regional variation in climatic selection pressures, and further that more similar tree genotypes support more similar community phenotypes. In support of this hypothesis, we found that 54.5% and 55.1% of the variation in climate space could be attributed to $K = 3$ and $K = 6$ genetic groups, respectively (perMANOVA $R^2 = 0.55$, $p < 0.001$). The first two PC axes explain 59.7% of variation among ecotypes (Figure 6) and reveal several notable patterns of niche divergence. The Utah High Plateau (UHP) ecotype is characterized by colder winters and the greatest temperature seasonality and dry quarter precipitation. In contrast, the Central California Valley (CCV) ecotype inhabits the greatest precipitation seasonality, highest winter precipitation, and greatest summer aridity. The Sonoran Desert (SD) ecotype's climate niche is moderate with respect to precipitation seasonality, with the summer monsoon from the Gulf of México and winter storms from the Pacific bringing roughly equal contributions of annual precipitation. This ecotype also inhabits the hottest summer temperatures, longest growing season, and greatest annual climate moisture deficit (i.e., largest sum of monthly differences between evaporation and precipitation). While differences in climatic selection pressures may influence host genetic divergence, associated communities ultimately cue into functional traits of the tree. Supporting this prediction, we found that genetic and climate niche differentiation were also associated with differentiation in plant growth characteristics. Number of leaves, leaf area, twig diameter, and twig length based on 3-year growth collectively show significant differentiation among ecotypes (ANOSIM $R = 0.151$, $p = 0.01$).

We further investigated which environmental variables are most important in structuring leaf-modifying arthropods across southwestern North America. Similar to the population scale, climate explained 24.8% of the total variation in arthropod community structure across the whole macrosystem (i.e., all three primary *P. fremontii* ecotypes, $p = 0.001$). While many species are generalists present across all ecotypes, several species emerged as indicators most associated with specific ecotypes (Figure S3). The differentiation along the first PC axis, separating communities associated with SD and UHP ecotypes, is primarily driven by degree-days above 5 °C ($r = 0.71$) and the minimum temperature of the coldest month ($r = 0.56$). Along PC2, the segregation between CCV-associated and more geographically interior communities is primarily driven by differences in temperature and precipitation seasonality ($r = -0.65$, $r = 0.57$, respectively) and continentality ($r = -0.65$).

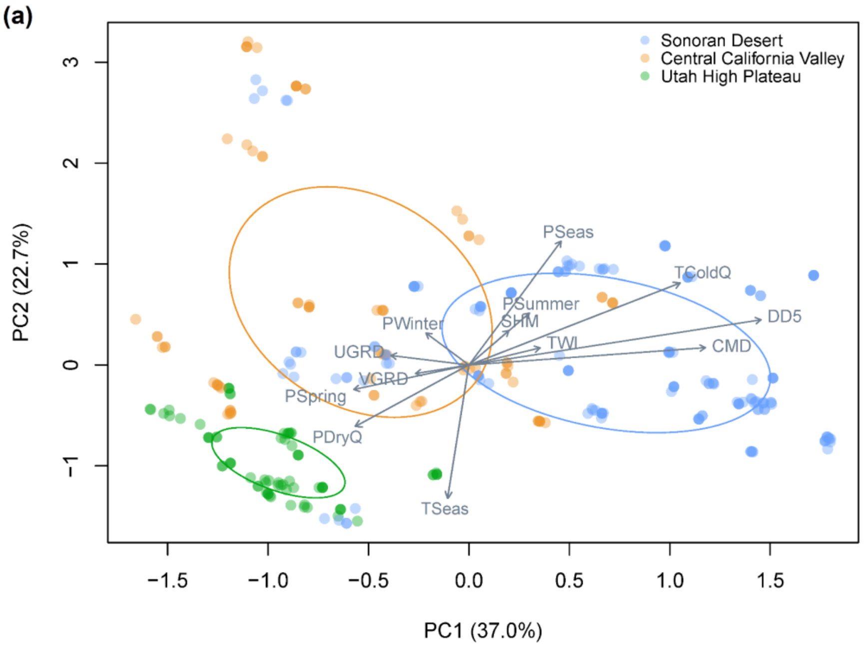

**Figure 6.** *Cont.*

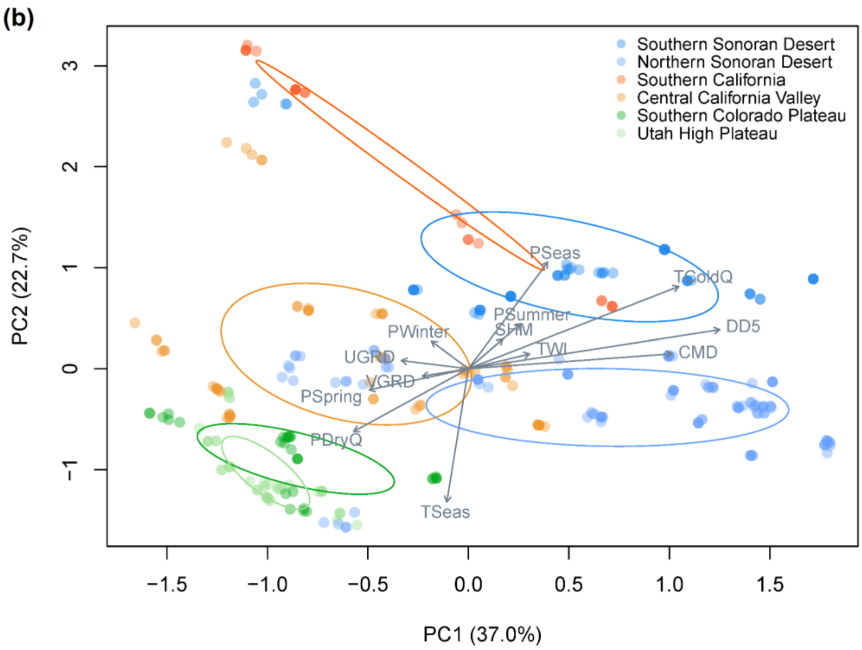

**Figure 6.** *Populus fremontii* ecotypes occupy significantly different climate niches, with the population genetic group explaining (**a**) 54.5% and (**b**) 55.1% of the variation in climate space for $K = 3$ and $K = 6$, respectively ($p = 0.001$).

## 4. Discussion

Here, we investigate the role of foundation tree species as drivers of macroscale community organization. By linking fine-scale genetic processes to continental-scale patterns, we aimed to integrate the 'genes to ecosystems' framework of community genetics with macrosystems ecology to bring an evolutionary perspective to broadscale biodiversity management [20]. As hypothesized, tree genetic variation is a significant factor driving macroscale biodiversity patterns for both communities investigated; however, we observed a stronger association for fungal endophytes compared with leaf-modifying arthropods, and the scale of the genetic organization significantly affected the ability to detect these patterns.

### *4.1. Climate as a Driver of Tree Local Adaptation*

Climate has long been known to be a primary driver of broadscale species distributions [13], and substantial evidence of local adaptation in response to climate has been observed in *P. fremontii* common gardens for traits related to growth, phenology, and temperature regulation [40,42,52–54,96]. The strong genetic divergence and environmental niche partitioning found here lend further support for local adaptation among ecotypes. Although our current study targeted more extensive sampling efforts throughout southern California, northern Utah, and México, analysis of genetic structure revealed that new samples are nested within the original three ecotypes defined by Ikeda et al. [39]. However, investigating the hierarchical substructure within each of the three primary ecotypes revealed additional partitioning, with substructure generally segregating along latitudinal gradients into northern and southern populations within each primary ecotype. We note that a fourth ecotype defined by Blasini et al. [42] based on drought and frost-adapted functional traits, Mogollon Rim (MR), is nested within the broader SCP ecotype defined here, which is inclusive of additional populations in southern Utah (Figure 3).

We detected significant niche divergence when considering both $K = 3$ and 6 genetic groups. Greater overlap is observed between the CCV and SD climate niches, relative to UHP (Figure 6a). The UHP ecotype occupies a substantially narrower and more divergent climate niche relative to the other ecotypes, even though samples spanned comparable latitudinal ranges. While both structure analysis and phylogeographic distance indicate strong neutral differentiation between northern and southern UHP populations, the climate niche differentiation between populations within this lineage is much less than that observed within the SD and CCV ecotypes (Figure 6b). In contrast, all four substructure groups within the latter ecotypes exhibit significant niche divergence. Previous studies coupled with the strong divergence observed here among climate niches and leaf and twig traits suggest that ecotypes of *P. fremontii* are locally adapted. As predicted, we observe that macroscale patterns of associated community organization reflect patterns of genetic differentiation of the host tree at the population and ecotype scales, and ultimately, functional trait divergence among tree ecotypes.

### 4.2. Predicting Macrosystem Properties

Supporting our hypothesis, we observed nonstationarity of tree genotype—community phenotype associations across genetic scales of organization. Individual-based models performed poorly at the macroscale; conversely, we detected significant tree genetic effects on community differentiation when considering the population and ecotype scales of genetic organization. Cushman et al. [49] found that the majority of genetic diversity is distributed within individuals in this species (75%), with only 3% distributed among individuals and 22% among populations. Given the very low genetic differentiation among individuals, it is perhaps not surprising that an association is undetectable when considering this scale of genetic organization.

At the population scale, tree genetic variation emerged as a significant predictor for both communities. Supporting our hypothesis, our data suggest that tree genetic variation has a stronger influence on endophytes (17%) compared to arthropods (13%), although this difference is relatively small. Furthermore, tree genetic variation and is the most important predictor of macroscale endophyte structure, explaining ~2× more variation than geography, with only a negligible independent contribution from climate. In contrast, the independent effect of environment explains nearly twice the variation (24%) in macroscale arthropod community organization relative to host genetics (13%). At the scale of ecotypes, host genetic variation is a significant driver of community organization (Figure 5), as is climate (Figure S3). However, for arthropods, the genetic contribution of host genetics is highly confounded with geography and climate at broader scales.

These findings highlight two common challenges of macrosystems ecology. First, the larger the scale, the fewer the independent system replicates, thereby limiting statistical power of inference at the broadest scales. Here the nature of the system (ecotypes of *P. fremontii*) precludes a sampling design that could achieve decoupling of genetic and climatic effects at the macrosystem scale. Second, while tree genotype—community phenotype relationships have been widely validated at local geographic scales (e.g., within common gardens), we observed a change in the strength of this association as we moved from individual, to population, to ecotype scales of genetic organization. This nonstationarity emphasizes that the predictive power and inferred strength of macrosystem relationships can depend on the chosen scale of analysis. Common garden studies have consistently observed that tree genotype predicts heritable community phenotypes in this species [21–24,97]. For example, tree genotype was found to explain 33% of variation in fungal pathogen community structure on *P. fremontii* [98]. Yet at the macroscale, we found geographic and climatic distance instead overwhelmed the genetic signal of association across individual tree genotypes; only when considering population and ecotype scales of genetic organization did the influence of tree genotype become detectable. Our findings emphasize the importance of taking a multiscale approach for understanding the functional drivers of macrosystem properties. This may include both coupling broadscale studies with fine-scale mechanistic investigations (e.g., common garden studies) and considering different scales of inference (e.g., geographic and genetic scales).

Community properties like diversity, stability, and structure are often viewed as emergent properties, because they result from complex interactions that cannot be easily explained by first principles [99]. However, Keith et al. [21] experimentally showed in common garden studies that arthropod diversity and community stability across years are heritable community phenotypes; some tree genotypes innately support richer or more depauperate communities that are more or less stable across years, respectively. Wimp et al. [97] also found that different tree genotypes support different communities; thus, the greater the genetic diversity harbored in foundation species, the greater community biodiversity they can support. Such findings, including the results presented here, argue that community properties arise in part as a direct outcome of first genetic principles in which the genetic-based multivariate phenotypes of plants can be used to predict associated properties of dependent communities at multiple scales.

### *4.3. Conservation Management Implications*

Arthropods have been particularly hard-hit by the global extinction crisis [100,101], with an estimated 40% of all insect species exhibiting precipitous declines [2]. Macroscale patterns of microbial diversity are less well understood, but no less important for supporting ecosystem services that all higher orders depend on [102]. Previous work has documented the disproportionately high biodiversity that *P. fremontii* riparian forests support relative to surrounding arid lands [103], and our findings highlight that tree genetic variation is a significant factor contributing to this biodiversity.

Fremont cottonwood is a foundation species of southwestern North American ecosystems, and the conservation of its associated biodiversity relies on preserving the remaining genetic variation harbored within this species. Yet, *P. fremontii* riparian forests are among the most threatened ecosystems in the US; as a result of water diversion, drought, and land-use changes, <3% of this species' pre-20th century distribution remains [104]. Climate change is predicted to further reduce *P. fremontii*'s suitable habitat, particularly for the UHP ecotype [39], which occupies the narrowest climate niche. Climate change will not only require species to migrate, adapt, or perish [105], but it is also likely to reduce tree productivity, which in turn alters productivity–diversity relationships and foundation species' capacity to support diverse associated communities [106]. Furthermore, as climate change often promotes invasive species such as *Tamarix* spp., these combined stressors can further reduce the productivity and distribution of native riparian forests [107]. Evans et al. [33] used common gardens of the same *P. angustifolia* genotypes reciprocally transplanted across a 1700 km latitudinal gradient from Arizona to Alberta to investigate phenotypic differentiation in functional traits associated with latitude of origin, emphasizing the role climate has played in divergent selection. They found evidence of arthropod segregation across different tree populations within the common garden environment that was consistent with tree trait divergence, and in particular, community metrics were positively correlated with tree productivity. These results lend support to the hypothesis that divergence in associated communities tracks genetically-based differences in phenology and growth traits of host plants at macrosystem scales.

As climate change continues to shift species distributions, an important future research question is understanding the degree to which community members will exhibit coordinated shifts or individual migration trajectories. Assisted gene flow is now a common strategy employed to address the increasing mismatch between local plant populations and ongoing climate change [108,109]. For example, the British Columbia Ministry of Forests reforestation policy recommends planting seed stock from approximately 2 °C warmer climate to achieve optimal future forest productivity goals [110]. Few studies have investigated the impact these shifts may have on associated communities, however, recent work by [111] suggests that optimal community transfer distances may not match those identified as optimal targets for their hosts. Keith et al. [111] surveyed arthropod communities on wild stands of *P. angustifolia* along a 90 km distance and 530 m elevation gradient, as well as communities on the same populations of trees planted in a low elevation common garden ~20 years prior. They found that a community transfer distance of >50 km and temperature increase >1.5 °C significantly altered community composition. Furthermore, our findings suggest that different communities more or less closely associated with the same tree are also likely to exhibit unique optimal transfer functions. Tree genotype is approximately twice as important as climate for explaining the geographic distribution of fungal endophytes, whereas climate is the primary factor structuring arthropod communities. When selecting restoration and reforestation stock, we urge practitioners to consider strategies that balance forest productivity targets with the maintenance of associated communities. Indeed, these goals are not mutually exclusive and are of particular concern as climate change increases tree stress and susceptibility to biotic agents. Maintaining native insect biodiversity provides natural pest and pathogen control, which in turn can feed back to support host productivity [112]. Climate-adjusted provenancing strategies (sensu [108]) select genotypes spanning a climate gradient biased towards predicted future conditions at a given planting site, yet also inclusive of a smaller fraction of local seed stock. This stepping stone strategy accommodates different community members with different migration rates, while also shifting optimum productivity towards future climate conditions, and hedging against uncertainty with diversity.

## 5. Conclusions and Future Directions

We identify three primary and six secondary *P. fremontii* ecotypes that exhibit distinct genetic and functional trait divergence associated with unique climate niches, which in turn support distinct arthropod and fungal endophyte communities. Tree genetic variation is a significant factor contributing to community differentiation at the continental scale. We hypothesize that the patterns of community differentiation observed here may have arisen as a result of multi-level selection in the context of community evolution, i.e., the change in community phenotypes through time in response to a geographic mosaic of spatially varying selection pressures [20,23,113], both biotic (genetics-based interactions among community members and trees) and abiotic (environmental variation). Future research is needed to test this hypothesis and gain insight into the adaptive mechanisms that have given rise to the observed community structure among ecotypes. Maintenance of regional biodiversity will require conservation genetic management of the unique diversity harbored within each of the six *P. fremontii* ecotypes. River network connectivity is positively correlated with genetic diversity in *Populus* [32]; therefore, maintaining existing riparian corridors and restoring degraded stretches will be critical for conserving adaptive potential of this foundation species and the diverse communities it supports. We investigated macroscale community organization within a ’genes to ecosystems’ framework, demonstrating the value of merging community genetics with macrosystems ecology, an objective that we consider critical for improving predictions of global change impacts on macrosystem properties and combatting widespread loss of biodiversity.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14050943/s1. Table S1: *Populus fremontii* collection information; Table S2: Environmental predictor variables; Figure S1: Principal component analysis of *Populus fremontii* genetic structure; Figure S2: *Populus fremontii* admixture frequency $q$ plots ($K = 6$); Figure S3: Arthropod differentiation by environment.

**Author Contributions:** Conceptualization, H.M.B., A.R.K., C.A.G., S.A.C., T.G.W. and G.J.A.; Methodology, H.M.B., A.R.K., J.B.H., H.F.C. and L.V.A.; Formal Analysis, H.M.B., A.R.K., J.B.H., H.F.C. and L.V.A.; Resources, H.M.B., A.R.K., J.B.H., H.F.C. and C.W.; Data Curation, H.M.B., H.F.C. and L.V.A.; Writing—Original Draft Preparation, H.M.B., A.R.K. and L.V.A.; Writing—Review & Editing, all authors; Supervision, C.A.G., S.A.C., T.G.W. and G.J.A.; Funding Acquisition, C.W., K.R.H., C.A.G., S.A.C., T.G.W. and G.J.A. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was supported by the NSF MacroSystems grant DEB-1340852 (K.H., C.G., S.C., T.W., G.A.), and NSF DBI-1126840 (T.W.) for establishing the Southwest Experimental Garden Array.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Genomic data for *P. fremontii* are available at NCBI's Sequence Read Archive (https://www.ncbi.nlm.nih.gov/sra, accessed on 24 March 2023), BioProject ID PRJNA868761. Twig fungal endophyte and arthropod community data, genetic distance matrices and sequence alignments, and environmental data are hosted on Dryad (https://datadryad.org/search, accessed on 24 March 2023).

**Acknowledgments:** The genomic library preparation and sequencing were carried out at the Environmental Genetics and Genomics Laboratory (EnGGen), Northern Arizona University, Flagstaff, AZ (https://in.nau.edu/gcf, accessed on 24 March 2023). We thank Ryelan McDonough for the laboratory assistance, and the Cottonwood Ecology & Community Genetics Group for their valuable feedback.

**Conflicts of Interest:** The authors declare no conflict of interest.

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