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Variation in Leaf Reflectance Spectra Across the California Flora Partitioned by Evolutionary History, Geographic Origin, and Deep Time

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Abstract Evolutionary relatedness underlies patterns of functional diversity in the natural world. Hyperspectral remote sensing has the potential to detect these patterns in plants through inherited patterns of leaf reflectance spectra. We collected leaf reflectance data across the California flora from plants grown in a common garden. Regions of the reflectance spectra vary in the depth and strength of phylogenetic signal. We also show that these differences are much greater than variation due to the geographic origin of the plant. At the phylogenetic extent of the California flora, spectral variation explained by the combination of ecotypic variation (divergent evolution) and convergent evolution of disparate lineages was minimal (3%–7%) but statistically significant. Interestingly, at the extent of a single genus (*Arctostaphylos*) no unique variation could be attributed to geographic origin. However, up to 18% of the spectral variation among *Arctostaphylos* individuals was shared between phylogeny and intraspecific variation stemming from ecotypic differences (i.e., geographic origin). Future studies could conduct more structured experiments (e.g., transplants or observations along environmental gradients) to disentangle these sources of variation and include other intraspecific variation (e.g., plasticity). We constrain broad-scale spectral variability due to ecotypic sources, providing further support for the idea that phylogenetic clusters of species might be detectable through remote sensing. Phylogenetic clusters could represent a valuable dimension of biodiversity monitoring and detection.

Plain Language Summary Related plant species often share inherited features, and we show that this is the case for the way the plant leaves reflect certain wavelengths of light. We collected leaf reflectance data from plants in a common garden where plants from across California are grown. Evolution explained more of the reflectance qualities of leaves than geographic origin of the plant species. These results provide support for the idea that remote sensing could help monitor biodiversity change by detecting groups of related plants.

Key Points:

- We collected leaf reflectance data from across the California flora from plants grown in a common garden
- Different parts of the spectra capture deeper evolutionary differences among plants and are more important than geographic origin
- This provides support for the idea that phylogenetic clusters of species might be detectable through remote sensing

Supporting Information:

Supporting Information may be found in the online version of this article.

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1. Introduction

Related species frequently resemble one another, having inherited features from their common ancestors. The magnitude of phylogenetic signal varies by trait, age, and ecological context (Blomberg et al., 2003; Cadotte et al., 2017). Phylogenetic signal is evident in many functional traits and also the biogeographic affinities of species (e.g., Griffith et al., 2019, 2020). In fact, it is uncommon for speciation events to result in shifts among biomes (Crisp et al., 2009; Donoghue & Edwards, 2014) and evolutionary history leaves a legacy in the structure and function of ecosystems (e.g., Griffith et al., 2019; Lehmann et al., 2014).

Phylogenetic signal is evident in the reflectance values of plants (e.g., Griffith & Anderson, 2019). Leaf reflectance spectra integrate information about the light-capturing physiology, leaf economics and anatomy, and energy/water balance of plants. In particular, hyperspectral reflectance across visible to shortwave infrared (VSWIR) wavelengths (380–2,500 nm) contains information ranging from pigment concentrations to structural and chemical attributes of vegetation (reviewed in Cawse-Nicholson et al., 2021; Cavender-Bares et al., 2020). The relationship between spectra and plant traits means that vegetation attributes can be projected across a wide range of species (e.g., Anderson et al., 2018), although there remain important challenges in scaling from leaves

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and species to pixels. Nevertheless, there is potential to identify related species using remotely sensed data as proposed by Griffith et al. (2020) and expanded upon in Anderegg et al. (2022).

An important and previously unanswered question that limits the utility of leaf reflectance spectra is the degree to which spectral differences among plants are associated with intraspecific variation versus species identity and phylogeny. How does the magnitude of variation in phylogenetic patterns in leaf reflectance spectra compare to variation due to average levels of within-taxa variation? Previous studies have considered this problem in terms of variability within preexisting spectral libraries and have been limited to resampling already spatially and taxonomically biased data to produce variability estimates. Instead, we collected new data from a pseudo-common garden where plants from across the California Floristic Province (CFP) were grown in the same location. This shared environment allows for spectral variation to be partitioned simultaneously relative to phylogenetic relatedness and the region of origin. By sampling plants grown in the same location, this approach controls for a degree of intraspecific variation due to phenotypic plasticity and allows us to ask, in aggregate, what proportion of spectral variation comes from ecotypic variation (e.g., local adaptation) as well as spectral differences among regions due to convergent evolution among lineages. This approach cannot distinguish between the latter two sources of variation or comment on the degree of phenotypic plasticity or seasonal variation. Instead, it allows us to constrain the magnitude of phylogenetic and ecotypic or convergent sources of spectral variation. Expanding on this question, we also conducted an assessment of phylogenetic signal across spectral regions to understand this variation in deep time.

2. Methods and Results

2.1. Study Area

We focused our study in the Regional Parks Botanic Garden (RPBG) which is located in Tilden Regional Park, Berkeley, CA, a part of the East Bay Regional Park District. The botanic garden is located at 37°53′34.61″N and 122°14′34.57″W (Figure 1). RPBG is approximately 10 acres but contains approximately 3,500 taxa representing about 130 plant families from across the CFP. RPBG is divided into sections that broadly represent the floristic subregions of the CFP as defined in The Jepson manual (2012) (Figure 1a).

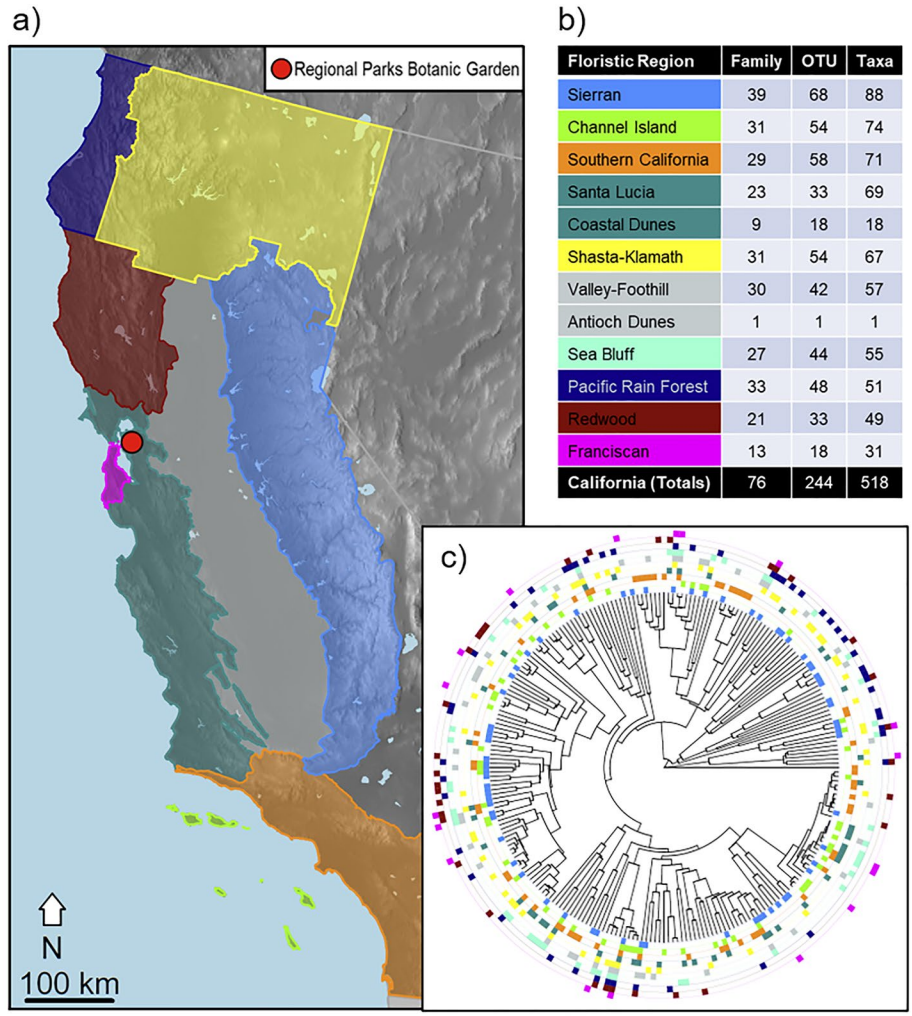
2.2. Sampling Design

RPBG presents the opportunity to sample species from across the California flora but grown in the same place. RPBG is not a true common garden study as plants are not grown from seeds under the exact same conditions. Plants at RPBG experience several sources of variation in conditions: for example, watering is conducted by staff in the interest of maintaining the health of the garden rather than standardization, there is microsite variation due to elevation and shading from neighboring plants, and plants are of differing ages. Furthermore, sampling at RPBG was limited to vegetation accessible from walking paths. Plants in the garden are often not selected as representative of regions but are likely to have been included because they caught the attention of a curator. Nevertheless, this is the closest available way to sample mature plants grown in the same location across an entire regional flora and is a valuable compliment to distributed data assembled from databases.

We focused our work on 10 regions of the CFP represented at the RPBG (Figure 1b). During the summer of 2020 and the early fall of 2021, we visited RPBG with a back-pack spectroradiometer (ASD Fieldspec 4 and Fieldspec Pro) with an attached leaf clip and plant probe with its own light source (part number A122327). Both spectroradiometers were recently calibrated to absolute radiance. From each accessible plant, we collected leaf-level reflectance spectra (380–2,500 nm, with resolutions of 3 nm in the VNIR, and 10 nm in the SWIR) from ~3 representative leaves). Many studies focused on collecting pure endmembers for crop studies will sample more leaves (e.g., corn genotypes) but our interest was in the ability to sample across the entire plant phylogeny in CA (Figure 1c) and so to enable this we focused on fewer representative leaves but often sampled the same species many times across different regions. This process resulted in a database of 3,823 leaf-level reflectance spectra taken from 518 taxa at RPBG.

2.3. Data Processing

We used a dated phylogeny from Thornhill et al. (2017) for all phylogenetic analyses. The Thornhill et al. (2017) phylogeny is based on operational taxonomic units (OTUs) which are taxonomic groupings based on molecular



Floristic Region	Family	OTU	Taxa
Sierran	39	68	88
Channel Island	31	54	74
Southern California	29	58	71
Santa Lucia	23	33	69
Coastal Dunes	9	18	18
Shasta-Klamath	31	54	67
Valley-Foothill	30	42	57
Antioch Dunes	1	1	1
Sea Bluff	27	44	55
Pacific Rain Forest	33	48	51
Redwood	21	33	49
Franciscan	13	18	31
California (Totals)	76	244	518

Figure 1. Regional Parks Botanic Garden (RPBG) and the regions of the (a) California Floristic Province represented in the (b) leaf reflectance spectra and (c) phylogeny. Operational taxonomic units (OTUs) are the molecular-based taxonomic groups created by Thornhill et al. (2017). Regions in panel (b) with the same color are labeled subsection at EBBG, and the coloring scheme links to panel (c), where the relatedness of sampled OTUs is shown with tip colors showing in which regions those OTUs are represented.

similarity. This phylogeny represents the flora of California reliably in biogeographic applications (more details in Thornhill et al., 2017). In our data set, the median OTU represented 1 species, but ranged up to 71 individual taxa (*Arctostaphylos*). To link species sampled from RPBG to the taxa in the phylogenetic tree, we used the R package "Taxonstand" to match synonymous epithets to accepted species names and then to the tree (Cayuela et al., 2012). Before analysis, continuum removal (division) for all spectra was conducted with the "prospectr" R package (Stevens & Ramirez-Lopez, 2022). This preprocessing step allows for better comparison among spectra captured from different spectroradiometers and emphasizes spectral features rather than the overall reflectivity of each sample (Clark & Roush, 1984).

2.4. Phylogenetic Signal

We considered calculating phylogenetic signal metrics for each reflectance band in our RPBG data set. Because studies have already looked at phylogenetic signal in a range of spectrally derived plant traits (e.g., Griffith & Anderson, 2019) and a wide range of raw spectral features (Meireles et al., 2020), we decided to start by corroborating these findings by calculating Blomberg's K (a common metric of phylogenetic signal that compares observed traits values to Brownian motion based on a tip-swapping procedure) for the first axis of a principal

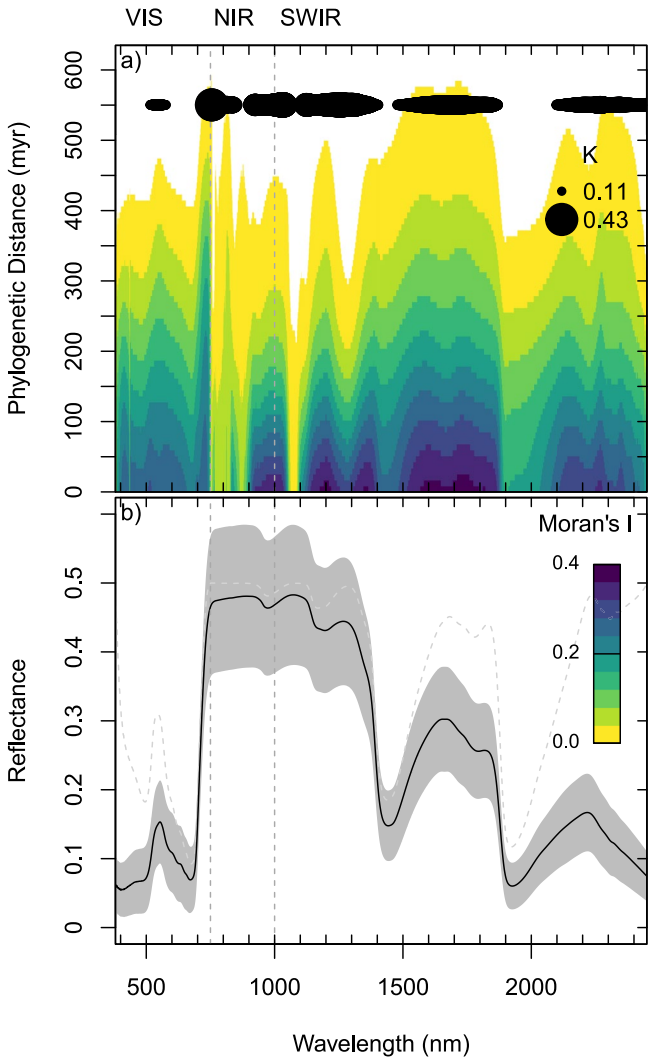


Figure 2. Phylogenetic correlograms for each wavelength in the Continuum Removed leaf reflectance data across the visible (VIS), near infrared (NIR), and short wave infrared (SWIR) shown as a surface of Moran's *I* values in panel (a). Higher values shown as darker blue shades indicate higher phylogenetic autocorrelation. These values go to phylogenetic distances in the hundreds of millions of years, with ages being half those values. For example, the dark areas associated with the red edge (690–740 nm) exhibit very deep phylogenetic autocorrelation. Blomberg's *K* values in regions with significant phylogenetic signal ($P < 0.05$) are overlayed as proportional symbols on panel (a) following Meireles et al. (2020). We report *K* values that are similar to Meireles et al. (2020) at comparable phylogenetic extent, and these *K* values align well with Moran's *I* values. Panel (a) is calculated from spectra subjected to Continuum Removal, and a similar pattern exists with raw spectra (Figure S1 in Supporting Information S1). Panel (b) shows mean leaf reflectance spectra in a black line and Continuum Removed spectra (rescaled 0–0.5) as a dashed light gray line. A visual exploration of phylogenetic variation at two wavelengths with contrasting patterns can be found in Figure S2 in Supporting Information S1.

components analysis of our spectra (PC1 explains 52% of variation, and together PC1–3 explain 84%) (Kembel et al., 2010). OTU mean values were used for these statistics. Similar to other studies, we also identified significant phylogenetic signal in leaf reflectance data ($K = 0.2$, $p = 0.001$).

We also wanted to know at what phylogenetic distance spectra remain similar to each other (i.e., at what distance does similarity decay). We also asked if this phylogenetic autocorrelation varied by spectral region. To do this, we computed phylogenetic correlograms for each wavelength to create a surface of Moran's *I* values showing at which wavelengths and evolutionary distances reflectance values are most autocorrelated (Figure 2a). These correlograms were calculated with the "phylosignal" R package (Keck et al., 2016) and again mean OTU values were used. We overlay significant *K* values over our phylogenetic correlograms to show that these align with the magnitude of phylogenetic signal reported in previous work when conducted at similar phylogenetic extents (e.g., Meireles et al., 2020).

2.5. Relative Importance of Taxonomy Versus Region of Origin

We approached the question of how spectra varied with region of origin and species identity with two approaches. First, we used phylogenetic generalized least squares regression with a Brownian motion covariance matrix to model the first eight PC axes of spectral variability (which together explain 95% of the variation in spectral data) as a function of region of origin and species identity (Paradis et al., 2004). We used an Akaike information criterion (AIC)-based model selection procedure (Table S1 in Supporting Information S1) showing that a model that includes both CFP region and species identity best captions variation in the spectra. Second, given that region was important, we conducted a variance partitioning using varpart() in the "vegan" R package (Oksanen et al., 2013) to determine how much variation in spectra could be attributed to phylogeny, region of origin, and species identity. For this analysis, we represented phylogenetic variability with a matrix of 17 PC axes that together explain 95% of the variation in phylogeny data. Most spectral variation was attributable to phylogeny with some additional variability being unique to individual species (15%) and a smaller portion being attributable to origin (Figure 3a).

To further explore the role of phylogenetic focus and extent, we also conducted our analysis in the context of species within one OTU, the genus *Arctostaphylos*, that was sampled frequently from different regions because the clade is a particular interest of RPBG. The *Arctostaphylos* genus is split into two monophyletic groups called the "small" ($n = 18$) and "large" ($n = 47$) clades. Our RPBG data set also captured tetraploid ($n = 16$) and diploid ($n = 42$) species. We partitioned variation in *Arctostaphylos* spectra by taxonomy (clade and species identity), CFP region, and ploidy level (Figure 3b). At this scale, much less variation in spectra could be explained, with taxonomy being the only important source.

2.6. Diagnosing Plant Groups With Spectra

Recent studies have proposed that the evolutionary relatedness of species can be used to improve our ability to remotely sense and model biodiversity (Anderegg et al., 2022; Griffith et al., 2020). Plant families are simply taxonomic classifications of related species and are an artificial starting point for spectral classification (Meireles et al., 2020) and new and flexible statistics are required for mapping phylogenetic clusters. As a starting point to assess the ability of spectra to classify

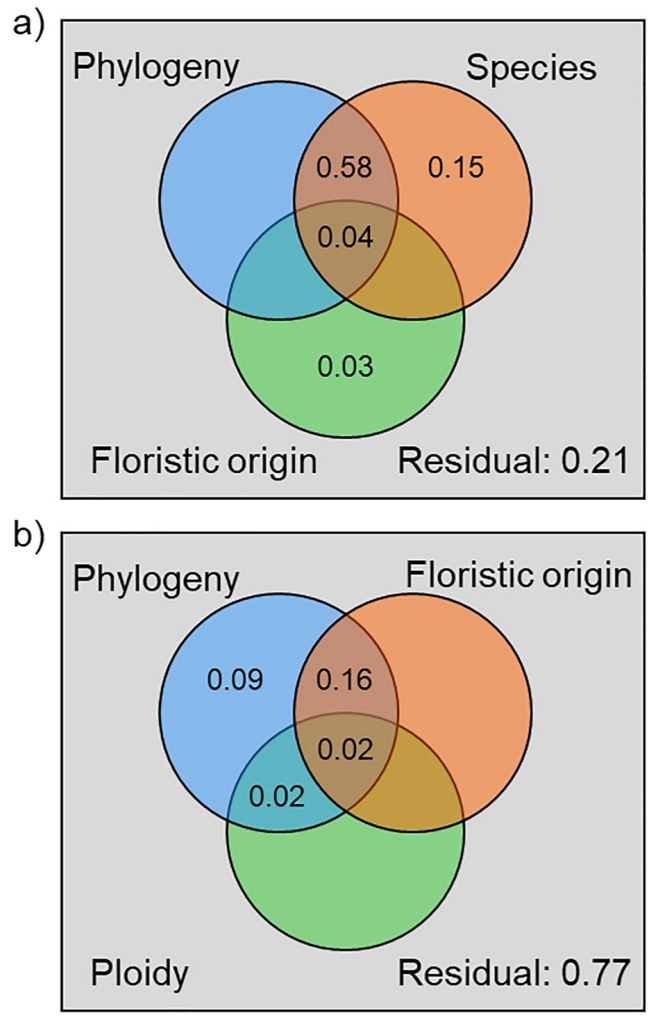


Figure 3. Variance partitioning of leaf reflectance spectral variability in (a) the represented California flora and (b) within the genus *Arctostaphylos* into phylogenetic/taxonomic sources, floristic origin (region of the California Floristic Province), residual variation, and in the case of panel (b), genome size.

phylogenetic clusters in the context of the California flora, we created partial least squares discriminant analysis (PLSDA) to model plant families as a function of spectra. We also conducted a complimentary analysis with the *Arctostaphylos* data to assess the ability to classify ploidy level and small/large clade identity (Parker et al., 2020; Wahlert et al., 2009). Promisingly we found that plant families could be moderately distinguished with spectra in the CA flora (74% accuracy and Kappa = 0.69) (Table S2 and Figure S5 in Supporting Information S1). At the scale of the genus *Arctostaphylos*, we were not able to distinguish the ploidy level of individual species, but there was a low to moderate ability to distinguish small and large clades (84% accuracy and Kappa = 0.55). PLSDA models were cross-validated as the purpose was to assess classification ability with a low sample size; however, it is recommended that external validation be performed if models were to be used for prediction (Griffith & Anderson, 2019).

3. Discussion

We found that patterns of leaf reflectance show similarity based on evolutionary relatedness in the California flora. We demonstrate this using a sample of plants that originate from each of the major biogeographic regions of the CFP (Figure 1) and including over 500 plant taxa representing over 70 plant families. Furthermore, we found that different wavelengths showed phylogenetic autocorrelation in reflectance that stretch back much farther in evolutionary divergence time than others (Figure 2). For example, the "red-edge" showed particularly high levels of autocorrelation at ages over 100 million years ago (i.e., distances over 200 myr) meaning that differences in

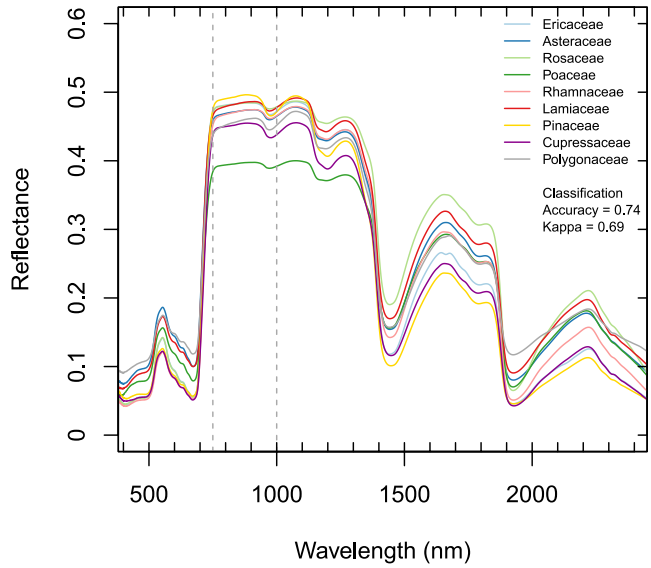


Figure 4. Mean leaf reflectance spectra of the major plant families represented at Regional Parks Botanic Garden with at least 20 individual samples. Classification statistics come from a partial least squares discriminant analysis and a confusion matrix is shown in Table S2 in Supporting Information S1. Classification was performed using Continuum Removed spectra shown in Figure S3 in Supporting Information S1.

this part of the spectrum are often inherited from common ancestors at the age of large splits within the Angiosperms and even differences in plant phyla.

Plants from the same part of the phylogeny but sourced from different regions of California did show differences in reflectance patterns, yet the magnitude of variation accounted for was fairly minimal (Figure 3a). This provides support for the idea that mapping approaches based on evolutionary relatedness of leaf reflectance may be generalizable across regions (Anderegg et al., 2022; Griffith et al., 2020). However, we show that additional leaf spectral variation existed at the level of species identity (i.e., below what was captured at the level of OTU relatedness) suggesting that error can be accumulated when approaches are applied to new regions that share evolutionary similarity but do not overlap completely in species identity. Still, over 4 times more variation was captured by phylogeny than by species identity. In addition, taxonomy was less important in explaining spectral variation at the scale of the genus *Arctostaphylos*, yet the other major potential sources of variation, such as ploidy and CFP region, explained no additional variability (Figure 3b). This suggests that even at higher taxonomic resolution evolutionary similarity may still be useful for detecting vegetation types or mapping aspects of vegetation diversity (Cavender-Bares et al., 2009; Cavender-Bares, Ackerly, et al., 2016; Cavender-Bares, Meireles, et al., 2016; Schweiger et al., 2018).

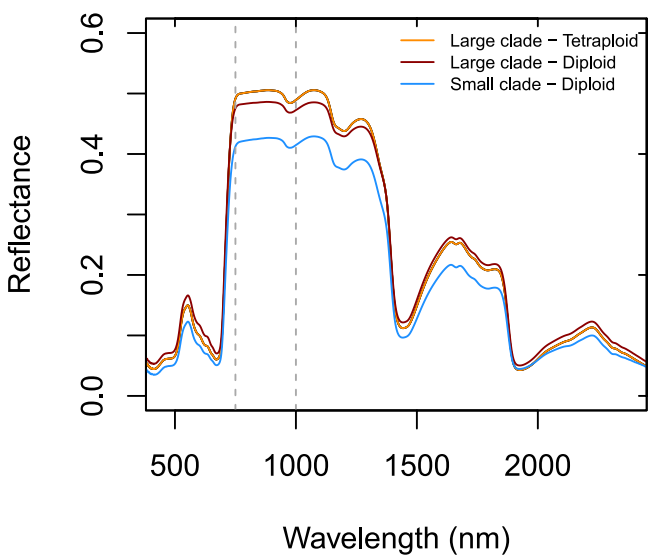


Figure 5. Mean leaf reflectance spectra for the large and small clades of *Arctostaphylos* separated by ploidy level for the large clade. See Figure S4 in Supporting Information S1 for Continuum Removed spectra.

As a preliminary assessment to inform future research, we assessed the ability of the leaf spectral reflectance data to classify plant groups. As previously discussed, new approaches are needed that balance phylofunctional distinctiveness, abundance, and spectral separability to better leverage spectral data for vegetation classification (Anderegg et al., 2022; Griffith, 2022, in review). Across the California flora, we found that simple taxonomic distinctions at the level of plant family could be moderately distinguished from their leaf reflectance spectra (Figure 4). Furthermore, even with a small data set, we were able to distinguish reasonably between two clades of *Arctostaphylos* (Figure 5). Where other studies have found that cytotype can be distinguished with leaf and canopy reflectance data, we did not find that ploidy was important in this data set (Blonder et al., 2020).

As previously mentioned, the experimental design (a pseudo-common garden study) does not allow us to capture other important sources of variation that will exist in remotely sensed data such as phenotypic plasticity, seasonal and developmental differences, or to distinguish divergent and convergent evolutionary patterns. Future studies could conduct more structured experiments, including transplants or observations along environmental gradients, to disentangle these sources of variation and include other intraspecific variation (e.g., plasticity). These could be combined with repeated sampling (e.g., the Surface Biology and Geology High-Frequency Time Series SHIFT campaign) to help separate intra-annual variability. Furthermore, scaling from leaf scans to remotely sensed pixels remains challenging. While we find moderate classification ability for plant families and minimal variability due to ecotypes, more work is needed to determine when phylogenetic clusters can be reliably retrieved at regional extents. Similarly, leaf types in our study and comparable studies include a wide range of leaf types (e.g., sclerophyllous, hairy, succulent) that make it difficult to obtain reliable leaf-clipped spectra or to scale these spectra to pixels. It could be interesting to compare spectra from our study to data sets comprised of spectra assembled by many different researchers.

Our study improves upon current literature in that we focus on taxa that have been selected from a single floristic province and are grown in pseudo-common garden. In this sense, our data represent a current best-available data set, but it also includes a wide range of limitations. As previously discussed, the data are not a true common garden study with plants of the same age class, and indeed there is significant microsite variation and potential bias in plant selection. We propose that valuable additions for future literature would include transplant studies as well as truly detailed and within-species sampling of key species and clades (e.g., *Arctostaphylos* spp.) that might better constrain and partition the variation in spectral features that we describe here. Furthermore, multivariate calibrations such as PLS are prone to overfitting (Griffith & Anderson, 2019) and studies hoping to project these models should externally validate them and acknowledge this fact (e.g., Blonder et al., 2020). We are not able to able to externally validate our exploratory models here, and their purpose is as a starting point for future work.

We provide evidence from the California flora that leaf reflectance spectra show phylogenetic autocorrelation and that these patterns persist across plants sourced from different biogeographic areas. Our results suggest that evolutionarily informed methods may be a promising way forward for hyperspectral remote sensing, such as the future Surface Biology and Geology program.

Data Availability Statement

All data are available as Supporting Information to this article and in Zenodo repository https://doi.org/10.5281/zenodo.7537164.

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