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Key Points:

- First retrieval of mycorrhizal type from imaging spectroscopy
- Mycorrhizal type can be mapped with accuracy ($R^2 = 0.92$) across disparate landscapes
- Improvement in spatial precision of roughly 10^4 over current methods

Supporting Information:

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

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Tree Canopies Reflect Mycorrhizal Composition

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Abstract Mycorrhizae alter global patterns of CO₂ fertilization, carbon storage, and elemental cycling, yet knowledge of their global distributions is currently limited by the availability of forest inventory data. Here, we show that maps of tree-mycorrhizal associations (hereafter “mycorrhizal maps”) can be improved by the novel technology of imaging spectroscopy because mycorrhizal signatures propagate up from plant roots to impact forest canopy chemistry. We analyzed measurements from 143 airborne imaging spectroscopy surveys over 112,975 individual trees collected across 13 years. Results show remarkable accuracy in capturing ground truth observations of mycorrhizal associations from canopy signals across disparate landscapes ($R^2 = 0.92$, $p < 0.01$). Upcoming imaging spectroscopy satellite missions can reveal new insights into landscape-scale variations in water, nitrogen, phosphorus, carotenoid/anthocyanin, and cellulose/lignin composition. Applied globally, this approach could improve the spatial precision of mycorrhizal distributions by a factor of roughly 10^4 and facilitate the incorporation of dynamic shifts in forest composition into Earth system models.

Plain Language Summary Mycorrhizae (plant root-fungus symbioses) play a central role in ecosystems, and differences in form and function between the two main types of mycorrhizae can influence ecosystem sensitivity to global environmental changes. While the symbioses are located belowground, we show here that they are also associated with subtle but detectable signatures in the structure and composition of forest canopies. As a result, the abundance of each mycorrhizal type can be mapped with both accuracy and precision across a diverse set of ecosystems using the emerging technology of imaging spectroscopy. This advance opens the door to a roughly 10,000x improvement in the precision of current global mycorrhizal maps, which should facilitate advances in several fields of Earth system science.

1. Introduction

Mycorrhizae play a pivotal role in multiple ecosystem processes, with far-reaching consequences for global Earth system processes. Recent discoveries have linked differences in mycorrhizal type to carbon and nutrient cycling and ecosystem sensitivity to CO₂ fertilization (Bennett & Classen, 2020; Corrales et al., 2018; Steidinger et al., 2019; Terrer et al., 2016) and nitrogen deposition (Averill et al., 2018; Jo et al., 2019; Midgley and Phillips 2014; Quinn Thomas et al., 2010), as well as biodiversity (Jiang et al., 2021; Powell & Rillig, 2018). Globally, two types of mycorrhizae predominate in forests: arbuscular mycorrhizae (AM) and ectomycorrhizae (EM). AM-dominated ecosystems tends to differ from EM-dominated ecosystems in traits such as foliar *N* isotopes (Craine et al., 2009), *P* uptake (Jansa et al., 2011), leaf mass area (Powell et al., 2017; Z Shi et al., 2020), leaf phenology (Key et al., 2001; McCormack et al., 2015), and rate of carbon and nutrient cycling (Keller & Phillips, 2019; Phillips et al., 2013; Read, 1991; Read & Perez-Moreno, 2003)—although important contingencies also exist (Koele et al., 2012). Most tree species form mycorrhizal associations of one and only one type, so maps of tree-mycorrhizal associations (hereafter “mycorrhizal maps”) could easily be made if the species and location of all trees on Earth were known. Unfortunately, this is not possible for most landscapes or at global scales.

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As a result, current global mycorrhizal maps are coarse (10^5 m scale) and correlative, rooted in indirect associations with variables like regional climatology and soil type, or species distribution models (Soudzilovskaia, Vaessen, et al., 2019; Soudzilovskaia, Van Bodegam, et al., 2019; Steidinger et al., 2019; Sulman et al., 2019). Limitations in both precision and accuracy (e.g., $\pm 17\%$ – 20% at the 90% confidence level, [Soudzilovskaia, Vaessen, et al., 2019; Soudzilovskaia, Van Bodegam, et al., 2019]) of these estimates has the potential to seriously impact our understanding of global climate and biogeochemical processes (Terrer et al., 2016). Fisher et al., (2016) suggested one approach to improve these models using optical remote sensing, introducing the concept that mapping mycorrhizal type from canopy reflectance might be tractable, even if large-scale mapping of tree species is not. It may thus be possible to use remote sensing to quantify the abundance and distribution of each mycorrhizal type within landscapes containing multiple tree species using optical measures of canopy composition, rather than (or in addition to) the indirect associations described above.

While results from Fisher et al. (2016) were promising, they were limited by the multispectral sensor available for observation. New imaging spectroscopy data offer an intriguing solution (Chapman et al., 2019). The capacity of these instruments vastly exceeds older multispectral sensors, capturing subtle spectral differences linked to canopy chemistry (Asner, 1998; Mutanga & Kumar, 2007; Mutanga & Skidmore, 2007; Serrano et al., 2002), structure (Bergen et al., 2009), and environmental conditions (Cavender-Bares et al., 2020; Swatantran et al., 2011). If mycorrhizal signatures prove sufficiently distinct to consistently differentiate AM and EM plants, this new approach could transform both the precision and accuracy of existing approaches and transform our ability to account for dynamic shifts in forest composition within Earth system models.

Here, we present the first direct retrieval of mycorrhizal type from imaging spectroscopy. By applying cross-validated partial least squares (PLSs) regression to 143 AVIRIS flightlines and field observations of 112,975 trees spanning $\sim 8,000$ km and a broad ecoclimatic amplitude, we show that continuous gradients of AM versus EM associations can be accurately discriminated within and among highly diverse landscapes at 10^1 m scale resolution—a 10^4 scale improvement in our knowledge of these systems. From tropical to temperate, and from sea level to 3,000 m, this challenging test reveals imaging spectroscopy's potential to revolutionize observation, modeling, and prediction of an Earth system process with global importance.

2. Results

One of the most challenging of the six sites (Harvard Forest) is illustrated in Figure 1. This site contains a combination of monotypic clusters of plants forming AM associations, monotypic clusters of plants forming EM associations, and heterogenous areas spanning the AM-to-EM density continuum. Imaging spectroscopy was able to accurately discriminate AM-dominated (red), EM-dominated (blue) and mixed (yellow) areas within the site using a single universal model of spectroscopic differences in mycorrhizal trees. Both abrupt and dispersed spatial gradients were observed in the field data (Figure 1: top-left; points on a visible image), retained by the gridding process (Figure 1: bottom-left), and accurately captured by the imaging spectroscopy-based model (Figure 1: bottom-right). Comparable results were observed across all six sites. Cross validation was performed using test/train quantiles ranging from 10%/90% to 90%/10%, both with and without normalization for fraction of samples derived from each site. Models were also examined which excluded entire sites or pairs of sites. The robustness of the result suggests that highly accurate and precise information about mycorrhizal geography can be reliably obtained from imaging spectroscopy, even across a wide range of vegetation types and climates. More details on modeling and cross validation are included in the supporting information.

Averaged over all sites, AM and EM spectra revealed differences in foliar chemistry. AM canopies were found to generally absorb more light than EM canopies in wavelengths related to key biogeochemical properties (Figure 1: top-right). At 450–680 nm, AM spectral asymmetry suggests more absorption by non-chlorophyll agents like carotenoids and anthocyanins than EM, consistent with previous experimental and observational studies (Averill et al., 2019; Baslam et al., 2013; Fester et al., 2002; Lingua et al., 2013; Rosling et al., 2016). Leaf N indicators are divergent: lower leaf N is suggested at 680–770 nm (Mutanga & Skidmore, 2007), but higher leaf N is suggested by the steeper AM spectral slope at 1680–2100 nm (Serrano et al., 2002). Previous

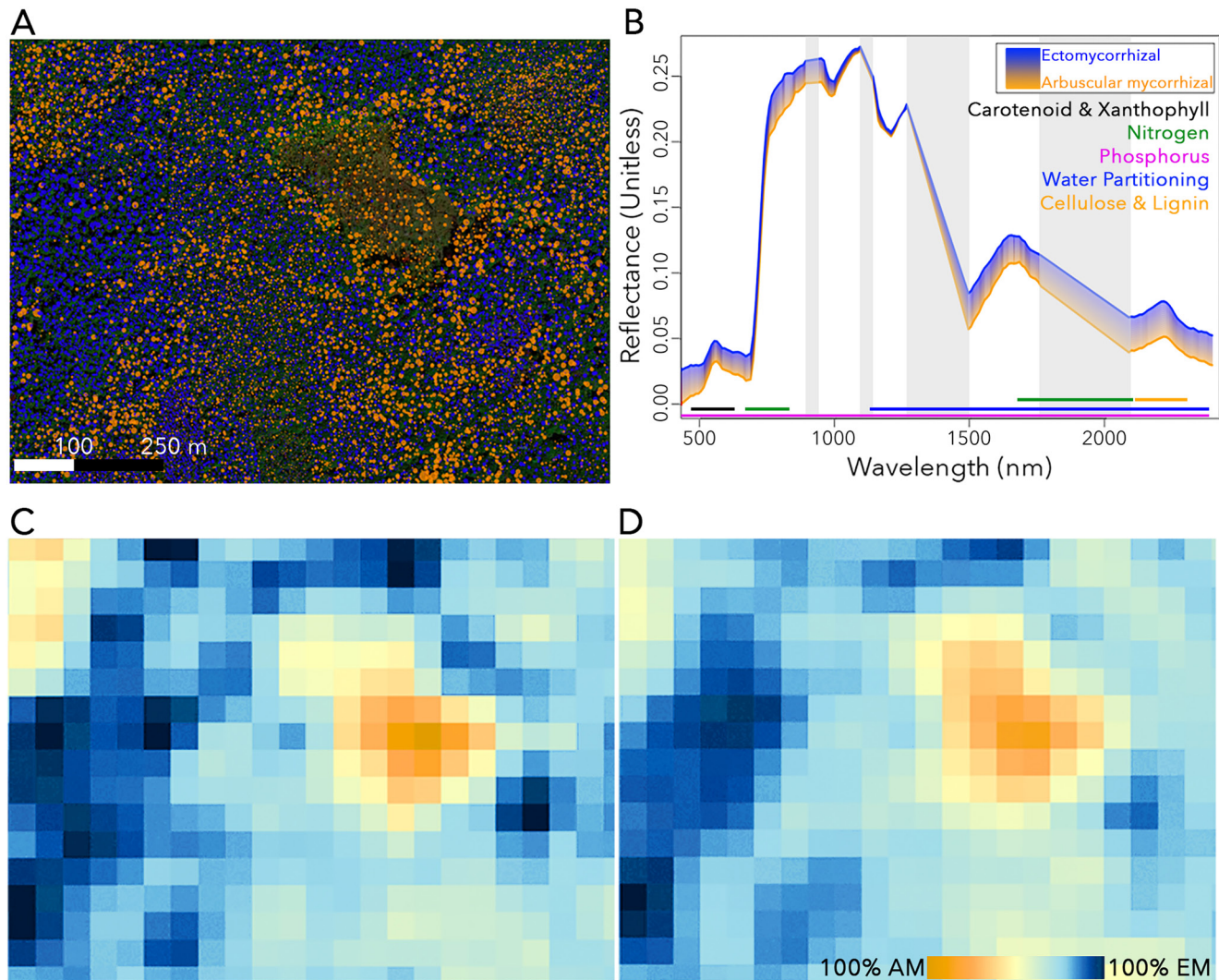


Figure 1. Imaging spectroscopy captures spatial variability in tree-mycorrhizal associations. Site shown is Harvard Forest, which had the greatest compositional heterogeneity. Field observations were scaled by basal area and color coded by mycorrhizal type (a; orange points: arbuscular mycorrhizal (AM); blue points: ectomycorrhizal (EM); underlying image: true color airphoto). Mean AM versus EM spectra across sites reveal biogeochemically relevant differences (b; horizontal lines: key spectral regions, gray bars: atmospheric absorption windows). Measurements were gridded at 30-m (c) and compared to predictions from imaging spectroscopy (d).

process-based studies suggest that one explanation for this may be differences in organic versus inorganic N (Averill et al., 2019; Phillips et al., 2013; Veresoglou et al., 2012).

Longer wavelengths revealed additional differences in canopy composition. At 1125–1300 nm, the combination of muted differences here along with greater differences at 1500–2500 nm suggests greater water partitioning towards the upper canopy for AM than for EM (Asner et al., 2006; Kannenberg & Phillips, 2017). The difference in canopy water partitioning-related bands between mycorrhizal types is a novel finding that has not been captured by previous observational studies. At 2230 nm, AM spectra suggest lower dry matter composition (e.g., cellulose, lignin), possibly due to higher quality AM leaf litter compared to EM litter (Asner, 1998; Keller & Phillips, 2019; Phillips et al., 2013; Read, 1991). No single wavelength is reliably associated with P, but multiple narrowband spectral indices, including the 970–990 nm (Ramoelo et al., 2013), 1730 nm (Cho et al., 2010), and 2015–2199 nm (Mutanga & Kumar, 2007) absorption features, are consistent in weakly suggesting that foliar P may be higher in AM versus EM plants, which would be consistent with the synthesis of Averill et al. (2018).

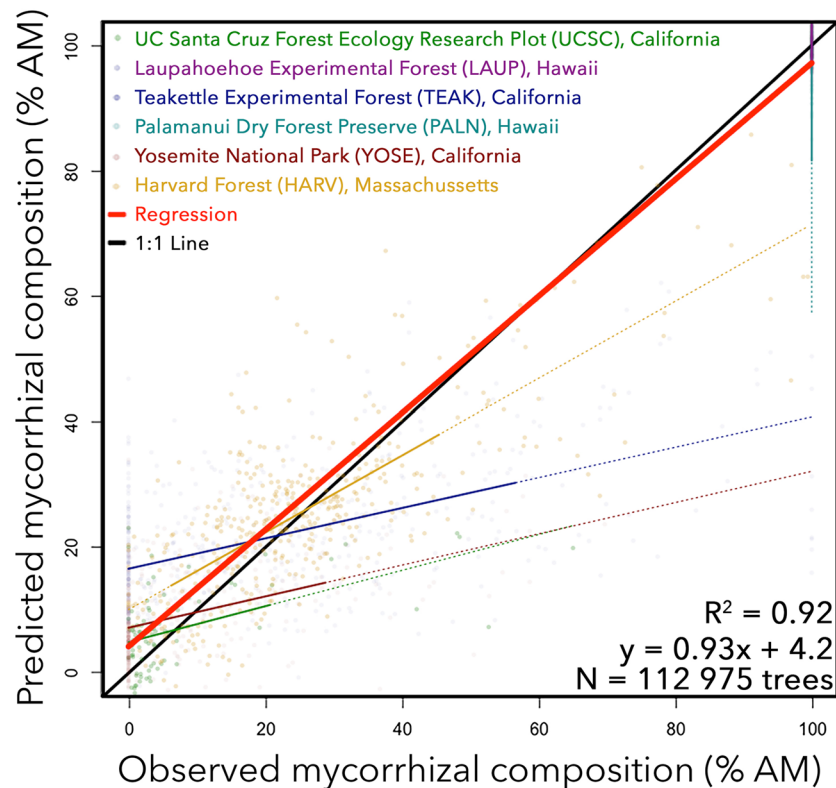


Figure 2. Imaging spectroscopy predicts tree-mycorrhizal associations for 112,975 in-situ measurements. Observed versus predicted basal-weighted fraction of arbuscular mycorrhizal (AM) associations. Each point represents the mean AM composition of a single 30-m pixel. A single model is used to make all predictions. Data span diverse bioclimatic conditions and 0%–100% AM/EM composition. Overall regression: thick red line. Site-specific regressions: thin colored lines (covering 10%–90% quantiles) and dotted lines (extending to maximum and minimum data values for each site). 1-to-1 line: black.

The relationship between mycorrhizal type and imaging spectroscopy observations was consistent across sites. Specifically, the strong relationship ($R^2 = 0.92$, $p < 0.05$) between spatial variability in canopy reflectance and field-observed mycorrhizal composition was observed to hold using a universal model (Figure 2). The database contained some sites (Palamanui and Laupahoehoe) dominated by nearly monotypic stands of AM trees, others that were largely EM-dominant (Teakettle and U.C. Santa Cruz), and yet other sites (Harvard Forest and Yosemite) with heterogeneous assemblages of both AM- and EM-forming tree species. No one site was observed to perform significantly better or worse than any other site using the general model. Landscapes with mixed mycorrhizal composition are more challenging to model accurately than those with nearly pure AM or EM associations (e.g., $R^2 = 0.41$ with pure pixels excluded). However, the mixed pixels results remain statistically significant, and pure pixel results are ecologically meaningful in and of themselves.

Topography and climate are two of the predictors most commonly used to estimate mycorrhizal composition (Bennett & Classen, 2020; Fisher et al., 2016; Steidinger et al., 2019). We thus conducted an analysis of these predictors versus mycorrhizal type, independently of the spectral analysis. For the sites in this study, topographic and climatic predictors demonstrated substantially less consistency than imaging spectroscopy-based predictors. For instance, at the temperate forest site with the greatest mycorrhizal tree diversity, arbuscular mycorrhizal abundance is negatively ($r = -0.46$; $p = 0.05$) correlated to elevation supporting information S1, gold). However, at the coastal mixed-evergreen Mediterranean-climate forest site, essentially no relationship ($r = +0.16$; $p = 0.05$) is found (Supporting information S1, green). Climate-based correlations yield the expected macroscale relationships (i.e., the sites with tropical climates are dominated by AM; temperate sites are not), but cannot inform within-site variability (Supporting information S1). Compared

to these approaches, imaging spectroscopy offers the ability to generalize across large spatial extents at fine spatial resolutions.

3. Discussion

Imaging spectroscopy-based mycorrhizal maps have the potential to significantly advance our understanding of Earth system processes (M. Shi et al., 2016, 2019). For instance, one outstanding question in mycorrhizal ecology is the extent to which climate change influences fungal-plant interactions. Geographic limitations of mycorrhizal data (e.g., 92% of studies have been conducted in the northern hemisphere) have seriously limited our ability to address this question (Bennett & Classen, 2020). Once global imaging spectroscopy data are available, the effect of this geographical study bias will be greatly reduced. In addition, the results presented here suggest that it may be possible to study time-varying mycorrhizal properties (Fisher et al., 2016), enabling answers about change in response to climate, disturbance, and other stressors. Another outstanding question is the relative global abundance of AM and EM plants—for instance, recent analysis of forest inventory data has also estimated that EM trees represent only 2% of tree species but may constitute as much as 60% of all stems on Earth (Steidinger et al., 2019). Global imaging spectroscopy could extend this observation beyond the locations of forest inventory plots and potentially detect as-yet unknown gradients and abrupt transitions in terrestrial ecosystems. Further disputes could also be addressed, such as those regarding the abundance of EM trees in tropical ecosystems (Corrales et al., 2018) and their relative role in determining leaf litter decay rates (Keller & Phillips, 2019) and nutrient cycling (Cheeke et al., 2017; Rosling et al., 2016; Veresoglou et al., 2012). Direct estimates of foliar traits can inform and potentially resolve such disagreements—and generate many more.

While the potential value of imaging spectroscopy for Earth system science is clear, complexities are inherent in interpreting canopy reflectance. Each measurement fundamentally integrates a complex amalgamation of plants, shadows, litter, and soil (Sousa & Davis, 2020). Subcanopy stems can be obscured by higher stature trees. Structural variables like gap fraction and leaf area can confound biochemical interpretations based on reflectance alone (Cavender-Bares et al., 2020). Absorptions overlap, resulting in nonuniqueness for many specific biochemical markers (Asner, 1998). Differences among forest canopy types not related to mycorrhizal composition, for example, broadleaf versus needleleaf scattering properties (Bicheron & Leroy, 2000; Gao et al., 2000), have the potential to overprint the reflectance signature of mycorrhizal type. We caution against over interpretation of inferences about foliar chemistry without additional field validation—but that said, we also note that the inferences made in this study are consistent with numerous observational and modeling studies (Averill et al., 2019; Baslam et al., 2013; Cheeke et al., 2017; Fester et al., 2002; Keller & Phillips, 2019; Lingua et al., 2013; Phillips et al., 2013; Read, 1991; Read & Perez-Moreno, 2003; Rosling et al., 2016; Veresoglou et al., 2012). Furthermore, while results are robust at the sites used in this investigation, we also caution against extrapolation without more extensive training. We note that other forms of mycorrhizal associations exist, most notably ericoid mycorrhizae (Cairney & Meharg, 2003; Read, 1991), and suggest detailed examination of the canopy-scale reflectance of ecosystems dominated by such associations as a promising avenue for future study.

Our findings raise salient points for future work. First, spectrally degrading the imaging spectroscopy data to simulate multispectral Landsat 8 bands causes significant accuracy degradation ($R^2 = 0.92$ vs. 0.71). But, spatially degrading the 15 m data to 30 m actually improved accuracy ($R^2 = 0.88$ vs. 0.92), which may be due to sensitivity to geolocation errors. Such observations suggest that a spaceborne imaging spectroscopy mission with global 30-m coverage may add more mycorrhizal insight than approaches which increase spatial but not spectral resolution (National Academy of Sciences, Engineering, and Medicine, 2018). Second, the combination of accuracy and detail possible with imaging spectroscopy suggests the potential for improvements in global biogeochemical models by providing accurate knowledge of the spatial and temporal distribution of mycorrhizal nutrient cycling pathways in heterogeneous systems (Steidinger et al., 2019; Terrer et al., 2016), especially when coupled with phenology (Fisher et al., 2016). Third, while forest inventory data are generally updated on annual or longer timescales, remote sensing allows dynamic updates, providing unprecedented insight into terrestrial ecosystem structure, function, and nutrient fluxes on our changing planet.

Taken together, the spectral evidence presented above has the potential to fundamentally advance our knowledge of global carbon and nutrient cycles. Because of the pivotal role that mycorrhizal type plays in interconnecting disparate components of Earth's biogeochemical system, this advance opens the door to a panoply of new Earth system science questions. For instance, inference of foliar chemistry differences in anthocyanin, carotenoid, *N* and *P* concentrations is consistent with some previous non-spectral studies of the same traits (Averill et al., 2019; Baslam et al., 2013; Phillips et al., 2013; Rosling et al., 2016), although complexities remain (e.g., Koele et al., 2012). What can we learn from global scale patterns of the geography of these foliar traits? It is well-known that temperate forests host a broad diversity of both AM and EM associations. What landscape-scale patterns exist in these types and their associated nutrient economies, and how do these correlate to other environmental factors like soil type? Perhaps most exciting, with global satellite imaging spectroscopy time series we will be able to examine change through time. What can we learn about the evolution of mycorrhizal and nutrient exchange processes as a result of anthropogenic impact, post-disturbance succession, and climate stress? This work paves the way for scientists to answer such questions—and more—with both high accuracy and global reach.

4. Materials and Methods

4.1. Field Data

Field surveys (112,975 trees) span diverse conditions, including two nearly monotypic AM tropical forests, a nearly monotypic EM temperate forest, and three temperate forests with mixed compositions. Measurements including stem position, basal area and species. Trees were determined to form AM/EM/both/neither associations by associating tree species with mycorrhizal type from the FungalRoot database (Soudzilovskaia, Vaessen, et al., 2019). All field-measured stems were used. Each stem was treated as a point measurement and weighted by basal area. These points were then aggregated to a 30-m grid and a stem-area-weighted average of fractional AM composition was computed for each 30-m grid cell. Details of each forest plot are given in the supporting information.

4.2. Imaging Spectroscopy Data

Surface reflectance data for 143 AVIRIS-classic flightlines covering the field sites were downloaded from <https://aviris.jpl.nasa.gov/dataportal/>. Orthorectification and geolocation errors were corrected. In sites with multiple flight lines, the mean reflectance spectra across all high-quality lines were computed and used as the predictor. Lines were manually inspected for quality. Images were chosen to maximize temporal consistency across sites. To standardize pixel dimension variations (~14–16 m) and compare to spaceborne missions, pixels were resampled to 30-m.

4.3. Modeling

Final model is based on cross-validated PLS regression with a 50% test-train split. Comparable results ($R^2 = 0.90$) were achieved with Random Forest regression, but PLS was found to be more robust to cross-validation. We used a universal (not site-specific) model, suggesting the possibility of extrapolation beyond these sites. Because the model was constructed for generalized global applications, we did not precondition the data by breaking the measurements into groups (e.g., broadleaf vs. needleleaf, evergreen vs. deciduous, or C3 vs. C4, etc.). Analyses of climatic and topographic variability were conducted independently to the primary PLS model. Further modeling details are provided in the supporting information.

4.4. Ancillary Data

One arc second (~30 m) gap-filled topography data produced by the NASA Shuttle Radar Topography Mission (product SRTMGL1v003) were obtained from the USGS EarthExplorer web portal at <https://earthexplorer.usgs.gov/> (NASA JPL, 2013). Data for 19 essential bioclimatic variables were downloaded at 2.5 arc minute and 30 arc second spatial resolutions from the WorldClim project at: <https://www.worldclim.org/> (Fick & Hijmans, 2017).

Conflict of Interests

The authors declare no competing interests.

Data Availability Statement

All data used for this research are available free-of-charge, without license restrictions. AVIRIS datasets used for this research are available from the AVIRIS Data Portal: <https://aviris.jpl.nasa.gov/dataportal/>. Climate and topography data used for this research are available from <https://www.worldclim.org/data/worldclim21.html> and <https://earthexplorer.usgs.gov/>, respectively. Plot data for the Laupahoehoe, Palamanui, Harvard Forest, U.C. Santa Cruz, and Yosemite sites are available from the Smithsonian Institution's ForestGEO Data Portal at <http://ctfs.si.edu/datarequest/>. Plot data for the Teakettle site are available at https://figshare.com/articles/dataset/BRID_data_txt/4749892.

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