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Imaging spectroscopy links aspen genotype with below-ground processes at landscape scales

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Fine-scale biodiversity is increasingly recognized as important to ecosystem-level processes. Remote sensing technologies have great potential to estimate both biodiversity and ecosystem function over large spatial scales. Here, we demonstrate the capacity of imaging spectroscopy to discriminate among genotypes of *Populus tremuloides* (trembling aspen), one of the most genetically diverse and widespread forest species in North America. We combine imaging spectroscopy (AVIRIS) data with genetic, phytochemical, microbial and biogeochemical data to determine how intraspecific plant genetic variation influences below-ground processes at landscape scales. We demonstrate that both canopy chemistry and below-ground processes vary over large spatial scales (continental) according to aspen genotype. Imaging spectrometer data distinguish aspen genotypes through variation in canopy spectral signature. In addition, foliar spectral variation correlates well with variation in canopy chemistry, especially condensed tannins. Variation in aspen canopy chemistry, in turn, is correlated with variation in below-ground processes. Variation in spectra also correlates well with variation in soil traits. These findings indicate that forest tree species can create spatial mosaics of ecosystem functioning across large spatial scales and that these patterns can be quantified via remote sensing techniques. Moreover, they demonstrate the utility of using optical properties as proxies for fine-scale measurements of biodiversity over large spatial scales.

1. Introduction

Current extinction rates are 100–10 000 times above background levels, primarily owing to anthropogenic land-use change and climate change [1]. The scale of human impact is unprecedented, but not unnoticed; human domination of the Earth's biological systems has been recognized for some time [2] and is likely to increase given the demands of a growing human population for food, fibre and fuel [3]. The ability of ecosystems to persist and provide services is contingent on the very biodiversity that is currently threatened [4–6]. Widespread recognition of the importance of biological diversity has led to the formation of international efforts to conserve biodiversity, such as the Convention on Biological Diversity (CBD). Identification of taxonomically and/or functionally diverse areas is a necessary step in achieving the CBD goals; however, measuring and comparing biodiversity over large areas is problematic [7]. In addition, it is clear that species richness, the most common biodiversity metric, represents only one facet of the diversity that is important to communities and ecosystems [6,8,9]. A host of recent research points to phylogenetic [10–12] and intraspecific diversity [13–18] as important drivers of both above- and below-ground processes. As a consequence, efforts such as the CBD recognize that forest biodiversity includes the diversity of trees as well as associated plants, animals and microbes, and can be considered at multiple levels of organization, from genetic to ecosystem [19]. Recent advances in remote sensing are well suited to quantify biodiversity across multiple levels of biological organization (within and across

species) as well as the consequences of such biodiversity over large spatial scales. The unique combination of detailed biodiversity and functional measurements with large spatial coverage places remote sensing technologies at the forefront of biodiversity research, particularly in an era of rapid global change. Here, we combine expertise from remote sensing, chemical ecology, population genetics and microbial ecology to assess genetic diversity, and the below-ground consequences thereof, in aspen forests of North America.

(a) Remote sensing of forest canopy chemistry

Remote sensing provides the capability to measure ecologically important forest parameters that drive ecosystem processes at large spatial scales [20]. Imaging spectroscopy platforms such as NASA's airborne visible/infrared imaging spectrometer programme (AVIRIS) provide high spectral resolution (224 bands) across a large spectral range (approx. 400–2500 nm), enabling the accurate measurement of a suite of canopy foliar traits that play key roles in governing ecosystem processes such as decomposition and nutrient cycling [21–22]. In particular, there has been considerable focus on the measurement of leaf nitrogen (N) and lignin concentrations via remote sensing, due in part to their important community- and ecosystem-level effects [23–26]. Spectra-derived estimates of canopy chemistry are not without challenges as spectral signatures reflect a combination of physiological, biochemical and structural properties [21,27]. Nonetheless, when properly applied, mapping from imaging spectroscopy holds promise for connecting canopy spectroscopy with plant traits important to ecology and evolution [22,28].

(b) Remote sensing of biodiversity

Concomitant with advances in measuring forest canopy chemistry are significant improvements in remote sensing of forest biodiversity [29,30]. Optical remote sensing has long been recognized as a pivotal tool in estimating species diversity [31]. Advances in technology that combine high spatial and spectral resolution data allow for the reliable identification of functional groups, individual species and sometimes even individual trees [29,32,33]. For instance, Asner *et al*. [34] used imaging spectroscopy (sometimes called 'hyperspectral') data to effectively map the distribution of invasive and native forest tree species in a Hawaiian rainforest. Recent remote sensing techniques have consistently resolved species-level biodiversity [35–38], even in high-diversity tropical ecosystems. Moreover, Asner & Martin [28,39], in putting forth the 'spectranomics' approach, have shown a strong relationship between remotely sensed chemical variation and phylogeny that also relates to community assembly. A remarkable attribute of this work is that it takes place in speciose tropical forests, and could potentially provide a basis to estimate biodiversity over large spatial scales in a system that is too diverse, and/or losing diversity too rapidly to measure via traditional ground-based methods. Here, we demonstrate that remote sensing can also be used to measure intraspecific genetic diversity in trembling aspen (*Populus tremuloides*) forests.

(c) Above- and below-ground linkages in aspen forests

Aspen are among the most widespread and genetically diverse plant species in North America [40,41]. They occur in mixed forests as well as monospecific stands that can extend continuously over broad areas; the largest individual organism known to science, the Pando genet, covers 44.3 ha in southern Utah, USA [42]. Western US aspen are often triploid and form expansive genets of genetically identical ramets [43–45]. Conversely, aspen in the Great Lakes region of the USA are rarely triploid [44], and form small genets that are often interspersed with mixed northern hardwood species. Western aspen stands have experienced recent and widespread episodes of mortality, primarily associated with long-term exposure to drought stress, which is likely to be exacerbated by future climate change [46,47]. This phenomenon, commonly referred to as sudden aspen decline (SAD), leads to the death of apparently healthy aspen stands in 3–6 years [48,49]. During a 1 year period from 2005 to 2006, the San Juan National Forest in Colorado experienced a 58% increase in area of recent aspen mortality [50]. That aspen decline and triploidy co-occur is not inconsequential; physiological traits associated with polyploidy may influence drought susceptibility, making regional declines in aspen a potential threat to genetic variation and persistence in aspen [44].

Genetic diversity within aspen is manifested as variation in plant chemistry, with different genotypes varying in leaf nitrogen, tannin, lignin and phenolic glycoside concentrations [51,52]. Variation in plant chemistry has long been associated with variation in herbivory [53], and is increasingly being linked to variation in below-ground processes [54–57]. Following from this, a growing body of evidence also suggests that within-species genetic diversity is important for below-ground processes in aspen [14,58–60] and other *Populus* species [61–63]. However, the spatial extent of the ecosystem consequences of intraspecific genetic diversity is unknown, because most research that explores how genetic diversity influences ecosystem processes has been conducted in plot-based studies. Such a restricted spatial scale of observation is not unique to intraspecific diversity experiments; the vast majority of biodiversity and ecosystem functioning studies are plot-based, with a mean plot size of $3\ m^2$ in terrestrial systems [64]. As a consequence, the strength of the continental-scale effects of intraspecific genetic diversity in natural systems remains unknown.

Here, we use imaging spectroscopy to investigate the ecosystem consequences of genetic diversity within trembling aspen ecosystems. Our goal was to test the capacity of remote sensing techniques to quantify forest genetic diversity and resulting below-ground microbial function across large spatial scales. Our specific objectives were twofold: (i) determine whether genotypic variation in canopy chemistry is important to below-ground processes at a large spatial scale, and (ii) determine whether spectroscopy can distinguish aspen genets and accurately estimate genetically mediated variation in both canopy chemistry and associated below-ground processes. We expected a close relationship between foliar and soil variation because of phytochemical differences among genets and the resulting differences in soil traits, as predicted from the literature. Given that spectroscopy is sensitive to chemical attributes of forest canopies [34], including many that we did not measure as well as others that have yet to be characterized, canopy spectra may better describe genetic variation than do foliar chemical traits. Following from this, forest canopy spectra may therefore indirectly relate to below-ground traits owing to the tight linkage between foliar chemistry and soil processes. We therefore sought to assess the ability of high-dimensional spectral variation to

serve as a proxy for variation in soil traits, and use spectroscopy to link canopy properties to soil properties.

2. Methods

(a) Field sampling

We sampled aspen forests in two ecoregions: the Great Lakes region of USA and Western USA. Field sampling was coordinated with AVIRIS flights in July 2009 (five transects in the Great Lakes) and August 2010 (four transects in the Western; figure 1). We identified aspen stands for sampling from Landsat-derived maps [65–67] and then confirmed in the field that sampling sites were located in monospecific aspen stands. Sampling was conducted in closed canopy forests. Within each transect, we established field plots composed of five 5×5 m crosses nested within a larger 60×60 m cross [68], such that each plot encompassed samples from 25 individual trees (figure 1). Full-sun-canopy foliage samples were collected in triplicate using shotguns or line launchers, and immediately placed in silica desiccant for later genotyping and chemical analyses. Each tree sampled for foliage was paired with a composite soil sample. Because soils can be heterogeneous over small spatial scales, soils samples for each tree consisted of three pooled 2.5×15 cm soil cores collected 1 m from the base of the target tree. Soil samples were sifted to 2 mm and frozen at -20°C within 24 h. We collected 1674 paired leaf and soil samples across 72 plots ($N_{tree} < 25$ for some plots owing to trees not present at the terminus of a cross). Leaf and soil samples were collected in July–August, with AVIRIS scene acquisitions occurring within one to two weeks following field sampling.

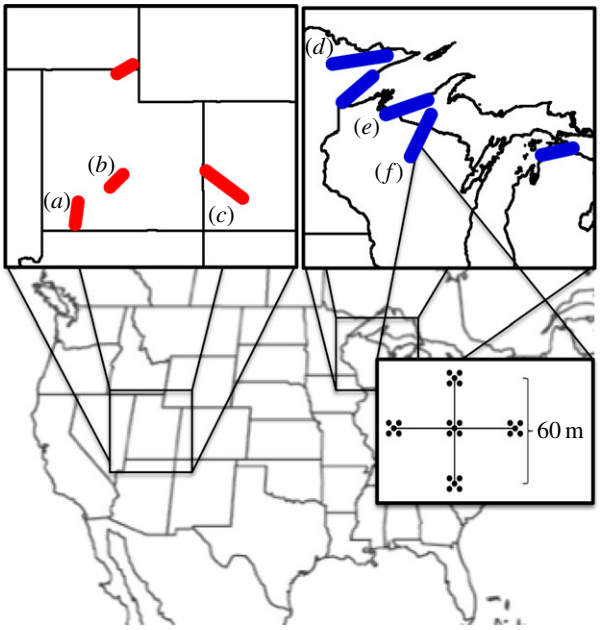

Figure 1. Map of AVIRIS scenes and sampling areas. Our sampling focused on aspen stands located in the Great Lakes and Intermountain West (Western) regions of the continental USA. Multiple AVIRIS scenes were collected in 2009 for the Great Lakes and in 2010 for the Western regions. Within each transect, we established sampling sites for paired foliage and soil samples based. At each site, five 5×5 m crosses were nested within a larger 60×60 m cross ($N_{tree} = 25$ per site). Labels (a–f) correspond to subpanels in figure 3.

(b) Leaf analyses

Leaves were processed for both genetic and chemical analyses. We used nuclear microsatellites to provide estimates of intraspecific diversity as they experience rapid evolution and display high amounts of population diversity. Genomic DNA was extracted from dried leaf tissue using a Qiagen DNeasy 96 Plant kit. Eight microsatellite loci were used to identify individual aspen genotypes: WPMS14, WPMS15, WPMS17, WPMS20 [69], PMGC486, PMGC510, PMGC2571 and PMGC2658 (http://www.ornl.gov/sci/ipgc/ssr_resources.htm) [70]. Reactions were prepared following Mock *et al.* [45] using primer-specific annealing temperatures provided in Callahan *et al.* [71]. PCR products were analysed on ABI sequencers using and LIZ500 size standards, and scored using ABI GeneMapper v. 4 (Applied Biosystems, Rotkreuz, Switzerland). Following Mock *et al.* [45], we pooled genotypes that differed by up to two alleles across all loci in order to avoid over-splitting owing to somatic mutations or amplification/scoring error.

Chemical analyses of leaf material included carbon, nitrogen, tannin and lignin assays. Total carbon and nitrogen were determined via flash combustion analysis on a FlashEA112 Elemental Analyser (ThermoFisher, USA). Condensed tannin concentrations (% dry mass) of leaves were determined following Madritch *et al.* [60] by extracting plant material with 70 : 30 acetone : water (containing 10 mM ascorbic acid) and assaying extracts via the *n*-butanol method of Porter *et al.* [72]. Aspen tannin standards were purified by the method of Hagerman & Butler [73]. Leaf lignin concentrations (% dry mass) were determined via the thioglycolic acid method [74] as modified by Suzuki *et al.* [75] using commercial lignin standards.

(c) Soil analyses

Soils were analysed for a suite of chemical and physiological parameters. Soil total carbon and nitrogen were analysed via flash combustion analysis as with leaf tissue above. In addition, we measured extractable soil ammonium and nitrate. Freeze-dried soils were extracted with 2 M KCl, and extracts were analysed for ammonium via the indophenol blue method with sodium dichloroisocyanurate as modified by Mulvaney [76], and for nitrate via reduction with vanadium(III) chloride and subsequent colorimetric analysis with Griess' reagent [77]. Soil microbes use various extracellular enzymes to access nutrients in complex organic compounds, depending on metabolic requirements and available nutrients [78]. We measured cellobiohydrolase and β-glucosidase (cellulose-specific), leucine aminopeptidase (protein-specific), phenol oxidase and peroxidase (aromatic-compound-specific) and urease (urea-specific) enzyme activity potentials. Assays were based on Sinsabaugh *et al.* [79] and Saya-Cork *et al.* [80]; see Madritch *et al.* [60] for details. The extracellular enzyme activity profile represents the functional activity of the microbial community [81], and may be more relevant to ecosystem functioning than is microbial taxonomic diversity [82]. In addition, enzyme activity profiles have been used previously to detect genotype-specific microbial functioning beneath distinct aspen genets [58–60].

(d) AVIRIS image acquisition and processing

NASA AVIRIS imagery was acquired from the ER-2 platform flown at 20 000 m above mean sea level on 13 July 2009 in the Great Lakes region and 25 August 2010 in the Western region. Data were provided as orthorectified, calibrated radiance images by the AVIRIS team at the Jet Propulsion Laboratory. Image pixel sizes range from 15 to 18 m depending upon ground elevation. We atmospherically corrected images using ATREM (TAFKAA [83]). Images were topographically corrected using the modified sun-canopy-sensor topographic method [84] and corrected for bidirectional reflectance distribution function (BRDF) using a quadratic function of the volumetric scattering term of the Ross–Thick BRDF model [85,86]. AVIRIS bands are

10 nm wide and cover a usable range 414–2447 nm. Our analyses used 182/224 bands; we excluded atmospheric absorption bands at 1333–1433 and 1782–1958 nm.

We calculated Normalized Difference Vegetation Index (NDVI, $[\rho_{841}-\rho_{658}]/\rho_{841}+\rho_{658}]$) to confirm that only closed canopy sites were included in our analyses (NDVI > 0.6 for all sites; electronic supplementary material, figure S1), and water band index (WBI, ρ_{899}/ρ_{967} [87]) to characterize variation in apparent canopy water content across AVIRIS scenes.

(e) Image pixel selection and sampling

Selection of AVIRIS image spectra (i.e. pixels) representative of each genotype took into account field plot layout (figure 1), pixel size and potential GPS and image spatial inaccuracies. We selected a 3×3 array of pixels around each tree's GPS-measured location, retaining only those pixels that met the following criteria: (i) the pixel contained five or more field-sampled trees, and (ii) at least 60% of the trees in that pixel were of the same genotype. This approach ensured that the selected pixels would be relatively genet-pure, and that our discriminant analysis (DA; §2*f*) of aspen genotypes included only those pixels that were dominated by a single genet of aspen. Across all field sites this resulted in a total of $n = 4327$ single-genet dominant spectra, representing 79 *distinct* multi-ramet genets (44 and 35 genotypes in Great Lakes and Western regions, respectively). To ensure that trait variation (spectra, foliar, soil) was comparable among analyses, we used a common set of genets by retaining only trees whose genets were preserved in the selection of image spectra. The tree- and soil-only analyses included data from $n = 706$ trees, which represent the same 79 genets for which we extracted image spectra.

(f) Statistical tools

Our primary objective was to determine the relationships between leaf spectra, leaf chemistry and soil chemistry. As much of the variation in leaf chemistry is genetically mediated in aspen, we also sought to determine whether canopy spectra could discriminate among aspen genotypes.

We first used generalized linear-mixed models (GLMMs) to confirm that leaf and soil traits varied by aspen genotype while accounting for spatial autocorrelation [88]. We then used canonical correlation analyses (CCAs) to assess the multivariate correlations between soil, foliar and spectral data, regardless of aspen genotype. CCA measures the strength of associations among two sets of variables (e.g. all spectra versus all foliar traits), where each dataset is transformed into new orthogonal functions that are maximally correlated [89]. Canonical correlation reveals the main dimensions (axes) of joint variability among pairs of datasets. The CCA yielded three sets of correlation coefficients important to our discussion. The first is the cross-correlation between corresponding canonical vectors generated for each of two matrices (e.g. spectra canonical axis 1 versus foliar trait canonical axis 1). The second and the third are the correlation coefficients between the two sets canonical of dimensions and each of their corresponding datasets (e.g. spectra canonical axis 1 versus individual AVIRIS wavelengths, and foliar trait canonical axis 1 versus individual leaf traits). GLMMs and canonical correlations were conducted using PROC GLIMMIX and CANCORR, respectively, in SAS v. 9.3.

We used DA to predict membership in aspen genets based on canopy spectra and on both above- and below-ground traits. DAs are useful to determine the capacity of continuously variable datasets (e.g. spectra, foliar traits, soil traits) to differentiate classes (e.g. genet), and then to classify correct group membership for new observations. All discriminant analyses were performed on 100 permutations of randomized subsets where 75% of the data were used for model calibration, whereas 25% were retained for validation. All results shown are average diagnostics from the application of the model to validation datasets. For spectral data, we used partial least-squares discriminant analysis (PLSDA, [90,91]) to account for the high dimensionality in the independent variables. PLS procedures project both the response and predictor variables into new latent vectors that maximize the prediction of the dependent variables via linear regression [92–94]. PLS is a core method in chemometrics and spectroscopy, and is designed to handle over-determined datasets wherein the number of independent variables is large and multicollinear [95]. For spectra-related DA, we set the number of components to $k - 1$, where k is the number of classes (e.g. genets) in the DA. Because the number of independent variables was much smaller for the soil and leaf traits (10 and four predictors, respectively), we used simple linear discriminant analysis (LDA) for soil and leaf traits. PLSDA and LDA were conducted in R using the caret and MASS packages [96,97].

We used Mantel tests [98] as complementary analyses to CCA to test whether multivariate matrices of pairwise dissimilarity in genetic, foliar and soil datasets were correlated. For example, is greater genetic distance between sites associated with greater spectral differences between sites? Partial Mantel tests [99] were used to test these relationships while controlling for spatial autocorrelation. For spectra, foliar chemistry and soil traits, we calculated pairwise distance in trait space as multivariate Euclidean distance of centred and standardized variables (to account for differences in measurement range for different variables) using the vegan package in R [100]. As a measure of genetic dissimilarity, we used the POLYSAT package in R to calculate Bruvo distances, which incorporate mutation and are well suited to quantify genetic diversity within species with mixed ploidy levels [101]. Partial Mantel tests were conducted in R using the ade4 package [102].

All analyses were conducted at two levels of geographical stratification: (i) all data, including samples collected in the Great Lakes region in 2009 and in the Western region in 2010, and (ii) independently for the Great Lakes and Western regions. The stratified analyses were conducted primarily to determine whether genets were spectrally separable both within geographical regions, where AVIRIS imagery was collected on the same date, as well as across geographical regions and years in which image acquisition characteristics may have differed. While not the focus of our study, climate varies between the two regions, and influences basic above- and below-ground processes. We used simple *t*-tests to describe how NDVI and WBI varied by region. For all analyses, statistical significance was assessed at $p < 0.05$.

3. Results

(a) Effects of region and genet on leaf and soil traits (generalized linear-mixed models)

Aspen varied in foliar tannin and lignin concentrations, with Great Lakes genets having notably higher tannin concentrations, and slightly lower lignin concentrations than did genets in the Western region (table 1 and electronic supplementary material, figure S2). While genet did influence leaf nitrogen, variation in leaf nitrogen was comparatively low and did not vary significantly by region. All leaf traits were strongly influenced by genet identity after correcting for the spatial autocorrelation of response variables using GLMM (table 1). In addition, after correcting for spatial autocorrelation, all soil traits were also influenced by aspen genotype (table 1). Soils beneath Great Lakes genets had less nitrogen, carbon and associated enzyme activities than

Table 1. Mean foliar and soil traits by sampling regions, and the effect of aspen genotype on foliar and soil traits after correcting for spatial autocorrelation. (Mean ± s.e. All traits were influenced by region at $p < 0.01$ unless indicated by 'n.s.' All genet effects $p < 0.001$).

traits	Great Lakes	Western US	genet effect
Tree			
leaf tannin (%)	13.69 ± 0.40	5.00 ± 0.21	$F_{78,627} = 30.8$
diameter at breast height (cm)	13.97 ± 0.49	24.20 ± 0.41	$F_{78,627} = 7.60$
leaf N (%)	2.40 ± 0.02	2.39 ± 0.02 n.s.	$F_{78,627} = 22.29$
leaf C (%)	49.48 ± 0.18	49.00 ± 0.07	$F_{78,627} = 4.26$
leaf lignin (%)	5.79 ± 0.16	7.04 ± 0.14	$F_{78,627} = 15.67$
soil			
soil N (%)	0.25 ± 0.01	0.64 ± 0.02	$F_{78,623} = 28.13$
soil C (%)	4.32 ± 0.22	10.00 ± 0.37	$F_{78,623} = 15.90$
NH_4–N ($\mu g\ g^{-1}$ dry soil)	8.26 ± 0.5	16.77 ± 0.96	$F_{78,626} = 14.75$
NO_3–N ($\mu g\ g^{-1}$ dry soil)	0.04 ± 0.01	1.52 ± 0.05	$F_{48,506} = 11.83$
β-glucosidase ($\mu mol\ h^{-1}\ g^{-1}$ soil)	107.46 ± 3.77	240.27 ± 8.95	$F_{78,626} = 32.40$
cellobiohydrolase ($\mu mol\ h^{-1}\ g^{-1}$ soil)	106.6 ± 4.67	109.44 ± 3.16 n.s.	$F_{78,626} = 18.93$
leucine aminopeptidase ($\mu mol\ h^{-1}\ g$ soil)	115.31 ± 4.04	180.98 ± 6.19	$F_{78,626} = 24.43$
urease ($\mu mol\ h^{-1}\ g^{-1}$ soil)	3.78 ± 0.21	8.45 ± 0.55	$F_{78,622} = 23.53$
peroxidase ($\mu mol\ h^{-1}\ g^{-1}$ soil)	0.38 ± 0.02	0.21 ± 0.01	$F_{78,626} = 16.30$
phenol oxidase ($\mu mol\ h^{-1}\ g$ soil)	0.21 ± 0.01	0.06 ± 0.01	$F_{78,555} = 12.19$

did soils associated with Western genets. Peroxidase and phenol oxidase activities, which are associated with polyphenolic breakdown, were higher in Great Lakes genets than in Western genets, corresponding with higher tannin content of above-ground inputs from Great Lakes genets.

(b) Spectral variation between regions

Great Lakes region genets had higher NDVI than did Western region genets (0.88 ± 0.001 and 0.77 ± 0.001, respectively, $p < 0.0001$), suggesting greater leaf area index and total foliar biomass in the more temperate Great Lakes region. WBI was also higher in the Great Lakes region than in the Western region (WBI: 0.943 ± 0.001 and 0.917 ± 0.001, respectively, $p < 0.0001$), indicating greater canopy water content at the time of imaging in the Great Lakes region than in the Western region. These results provide the basis for separating analyses of Great Lakes and Western genets owing to site differences, although absolute determination of whether differences in NDVI and WBI are due to year of AVIRIS imaging or site is not possible. However, the high and tightly distributed values of NDVI and WBI within each region (electronic supplementary material, figure S1) do indicate that our assumption of consistent canopy closure within region is reasonable.

(c) Links between spectra, leaf traits and soil traits (canonical correlation analyses)

CCAs addressed three questions: (i) are spectral traits related to foliar traits, as would be expected from the literature [25,103,104]; (ii) are foliar traits related to soil traits; and (iii) are spectral traits related to soil traits (i.e. can spectra be used as a proxy to estimate variation in soil processes)? Canonical correlation revealed strong multivariate relationships between canopy spectra and foliar traits, and between foliar traits and soil traits (figure 2, left side). In addition, we detected strong relationships directly between canopy spectra and soil traits (figure 2, right side). In all instances, we report the correlation coefficients of the first three canonical axes, as these describe the most variation in the paired datasets (labelled as 'canonical correlation' in figure 2 and see the electronic supplementary material, tables S1 and S2 for CCA details).

(d) Canonical correlation analyses: spectra and foliar traits

Canonical correlations demonstrate that spectral traits are related to foliar traits. The first canonical axis of spectra with foliar traits showed high correlations (positive and negative) with reflectance in green wavelengths (520–560 nm) that are associated with total pigment pools [105] and xanthophyll cycle processes [106], and in the region of the red edge (700–730 nm), with wavelengths that are associated with vegetative photosynthetic capacity (figure 2*a*, left side). Correlations were also apparent in the near infrared (NIR; approx. 780–1200 nm), likely related to canopy structure and leaf structure related to carbon compounds, and the short wave infrared 1 (SWIR1; 1440–1770 nm), wavelengths that are associated with phytochemistry [107,108], including tannins [109,110]. The first canonical axis describing leaf traits, which had the strongest relationship with the spectral data across all sites (figure 2, link between *a* and *b*), was related to condensed tannins, leaf nitrogen and lignin ($r = -0.98$, 0.42 and 0.43, respectively, figure 2*b*). These results indicate that foliar chemistry, and tannins in particular, are coordinated with canopy spectral properties.

Canonical correlations between spectral and foliar traits differed in direction and magnitude according to geographical region (i.e. all sites, Great Lakes, Western). Within the Great Lakes region, the first canonical dimension was most strongly

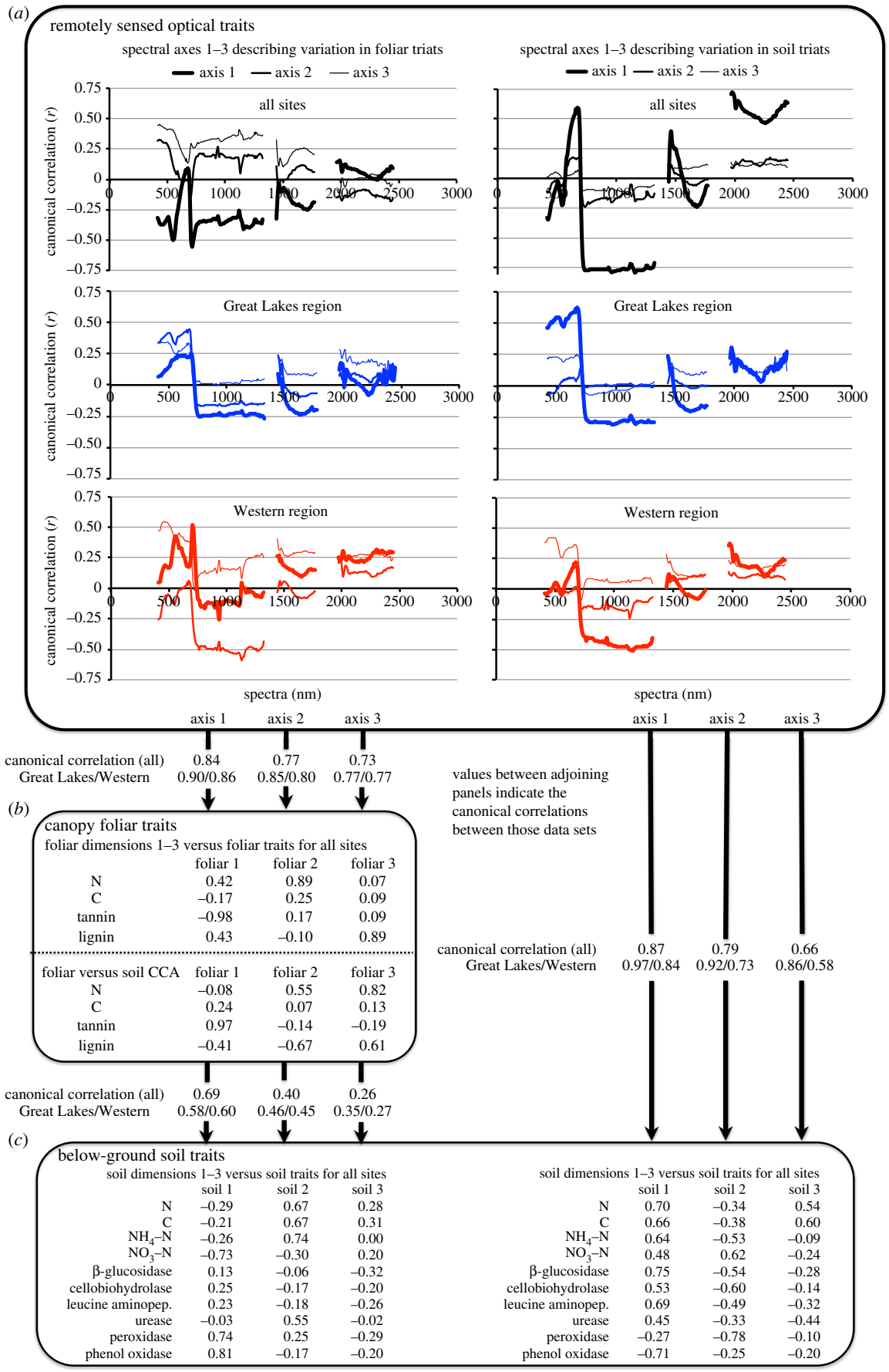

Figure 2. Conceptual diagram of connections between optical, foliar and soil traits. Canonical correlations describe the relationships between canopy spectra, canopy foliar traits and below-ground soil traits (left side of figure). Panel (*a*) displays the correlation of the first three spectral canonical axes with AVIRIS bands for all sites, Great Lakes and Western regions. The darkest line on each plot is of the first canonical variable, i.e. the linear combination of spectral data having the highest correlation with the linear combination of the second dataset (either foliar traits on left, or soil traits on right). Note that panel (*a*) displays many high negative correlations; absolute value indicates the strength of the relationships. Spectral canonical axes are then correlated with canonical axes that describe foliar traits, which are shown in panel (*b*). Foliar canonical variables are then correlated with canonical variables that describe soil traits, which are shown in panel (*c*). In addition to spectra–foliar–soil CCAs, we also describe the direct relationship between spectra and soils (right side of panel).

Table 2. Partial least squares discriminant analysis (PLSDA) and linear discriminant analysis (LDA) of aspen genet by spectra, foliar and soil traits. (Kappa values indicate the amount of agreement with genet classification as determined by microsatellite analysis and have a range of 0–1, with 0 being no agreement, and 1 being complete agreement. Unit of analyses indicated in parentheses.)

				mean kappa statistics of 100 simulations		
				spectral (pixel)	foliar (tree)	soil (tree)
	$N_{genotype}$	N_{pixel}	N_{tree}	PLSDA	LDA	LDA
all sites	79	4327	706	0.85	0.27	0.32
Great Lakes (2009)	44	896	175	0.89	0.18	0.32
Western (2010)	35	3431	531	0.87	0.37	0.33

correlated with tannins ($r = 0.97$; electronic supplementary material, table S2), with highest correlations across a wide range of wavelengths. The strongest correlations were in the green and red wavelengths and the NIR. The second canonical axis had high correlations with chlorophyll absorption features in the blue and red; and the third canonical axis, which had strong relationships with leaf N ($r = 0.88$; electronic supplementary material, table S2), was correlated with both the SWIR2 (greater than 2000 nm; known to be sensitive to N) and chlorophyll absorption features in the blue and red (figure 2*a*, middle left panel). The spectra–foliar canonical correlations for the Western clones differed from Great Lakes primarily in the strong association of spectra canonical axis 1 with wavelengths around the red edge (700–730 nm) that are associated with photosynthetic potential. Canonical axis 1 of the spectra–foliar trait relationship also correlated with wavelengths associated with pigment pools and xanthophyll cycle features (approx. 531 nm) and nitrogen-sensitive wavelengths in the SWIR2.

(e) Canonical correlation analyses: foliar and soil traits

As expected, foliar–soil canonical correlations demonstrated that foliar and below-ground traits were correlated, albeit more weakly than were spectral and foliar traits. The first canonical foliar variable, which was again correlated with tannin concentration ($r = 0.97$, figure 2*b*), was well correlated with canonical soil variables that describe variation in nutrient and enzyme traits across all sites ($r = 0.69$, figure 2, link between *b* and *c*).

(f) Canonical correlation analyses: spectra and soil traits

Lastly, to assess whether spectra could be used as a proxy for variation in soils, we used spectra–soil canonical correlations to relate spectra directly to soil traits. The first canonical dimensions of spectra that are related to soil traits was highly correlated with AVIRIS wavelengths at the red edge throughout the NIR to 1313 nm (wavelengths that are associated with canopy structure and carbon compounds), and with bands greater than 2000 nm (wavelengths that are associated with water content, nitrogen and phytochemicals; figure 2*a*, right side). Splitting the spectral data by geographical region influenced canonical correlations less for spectra–soil than for spectra–foliar correlations. The largest difference between geographical groupings was in the 2000–2500 nm of the 'all sites' stratification (figure 2*a*, top right panel), likely indicating the effect of regional differences in moisture or possibly also regional-scale differences in foliar chemistry. The first canonical dimension of spectra was highly correlated with the first canonical dimension of soil traits ($r = 0.87$, figure 2 linking panels *a* and *c*), which was related to multiple soil traits, including soil N and C, as well as β-glucosidase, leucine aminopeptidase and phenol oxidase activities (figure 2*c*, right side). These correlations indicate a potentially tight relationship between the spectra and soil traits; in fact, correlations between spectra and soil (figure 2, links between *a* and *c*) are stronger than are the links between foliar traits and soil processes (figure 2, links between *b* and *c*).

(g) Predicting aspen genotype with spectra (discriminant analyses)

Spectra discriminated aspen genets well across all sites and within each region (table 2). Moreover, that ability of spectra to classify aspen genets accurately was much greater than was the ability of either foliar or soil chemistry to distinguish genets. To a large extent, this is likely due to the richness of spectral data compared with the soil and foliar measurements, and high variability of aspen canopy reflectance across our sites (figure 3).

(h) Spectral distance and genetic distance (Mantel tests)

In addition to canonical correlation and discriminant analyses, we used Mantel tests to further explore the relationship between spectral, genetic, foliar and soil traits. In agreement with discriminant analyses above, partial Mantel tests revealed significant correlations between spectral distance and Bruvo's genetic distance, and to a limited extent, between spectral distance and foliar distance (table 3). Likewise, foliar trait distances were also correlated with Bruvo's genetic distance. Conversely, distance in soil traits was not correlated with either spectral or foliar distances. These analyses indicate that increasing genetic dissimilarity corresponds to increasing dissimilarity in spectral traits, a pattern that also exists in the foliar traits we measured, but non-existent in the soil traits.

4. Discussion

The scale of current anthropogenic global changes necessitates the application of novel technologies and interdisciplinary approaches to address fundamental questions in ecology. Here, we combine field-collected data spanning 2500 km of

Table 3. Partial Mantel correlations describing the relationship between spectral distance, genetic distance, foliar trait distance and soil trait distance (correlation coefficient, *p*-value). (Headings describe the first two matrixes included in the model, with the third being cartographic distance in all cases to account for spatial autocorrelation.)

	$N_{spectra}$	spectral versus genetic	spectral versus foliar	spectral versus soil	N_{tree}	genetic versus foliar	genetic versus soil
all sites	650	0.14, *0.001*	0.04, *0.031*	−0.01, *0.65*	705	0.03, *0.048*	0.03, *0.091*
Great Lakes (2009)	166	0.04, *0.013*	0.03, *0.203*	0.01, *0.403*	175	0.12, *0.013*	−0.06, *0.932*
Western (2010)	484	0.23, *0.001*	0.15, *0.001*	−0.06, *0.994*	530	0.02, *0.073*	0.01, *0.225*

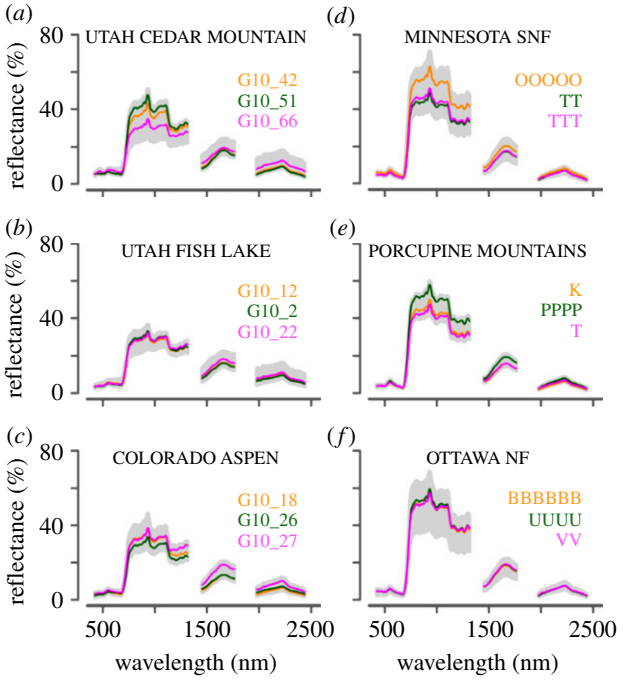

Figure 3. Within and across genet variation in spectra in multiple AVIRIS scenes. Grey-shaded areas represent the range of spectral variation among genets within an AVIRIS scene. Solid-coloured lines represent the average spectrum for representative genets. Each subpanel corresponds to a separate multi-AVIRIS scene area. Western areas are on the left and Great Lakes areas are on the right. Subpanel labels (*a*–*f*) correspond to AVIRIS scenes in figure 1. Alphanumeric codes within subpanels correspond to unique aspen genotypes. SNF, Superior National Forest; SF, State Forest.

aspen habitat with remotely sensed imaging spectrometer data. We demonstrate that aspen genets vary widely in canopy chemistry, and that variation in above-ground chemistry is associated with variation in below-ground chemistry and microbial activity. Moreover, we were able to use imaging spectroscopy data to estimate variation in field-collected metrics of aspen diversity, chemistry and below-ground processes. The ability of spectral data to describe genets and characterize variation in soil traits exceeded that of traditionally measured foliar chemistries, highlighting the effectiveness of highly dimensional spectral data for measuring biological systems over large spatial scales.

(a) Genetic mosaics of ecosystem functioning

Foliar and soil traits varied according to aspen genet identity across landscapes, consistent with smaller-scaled studies demonstrating variation in such traits among genotypes of aspen and other *Populus* species [14,41,59,61]. Unique to this study was that the influence of aspen genet on foliar and below-ground traits was apparent at broad spatial scales that spanned large amounts of environmental variation. The community and ecosystem consequences of intraspecific genetic diversity can be significant [8,111], but the relative importance of genetic diversity and the conditions under which genetic diversity is likely to be important remain unknown [8]. Here, in a clonal species that can dominate the forest canopy throughout much of its range, genotypic variation drives variation in above-ground chemistry, which in turn influences below-ground processes. We do not discount that edaphic factors such as nutrient availability also drive variation in aspen phenotype or below-ground processes, but the effects of genotype often exceed those of environment [52,112]. Likewise, while variation in temperature and moisture influence below-ground processes, foliar traits are often the strongest drivers of below-ground variation [113]. Our research indicates that across a large portion of its natural range, aspen genotype has a pronounced influence on chemical phenotype with significant below-ground consequences. In addition, there is also a strong connection between aspen genotype and spectral phenotype.

Biodiversity exists at all levels of biological organization, from genes to species to ecosystems, and the effects of genetic diversity can approach those of species diversity in some cases [8]. This may be the case in aspen-dominated systems of the species depauperate north-temperate zone, and losses in the genetic diversity in aspen systems could constitute a significant loss of ecological diversity and evolutionary potential. For instance, the rapid decline of aspen owing to long-term drought conditions may be a significant threat to the genetic diversity of aspen [44], with unknown consequences for above-ground herbivore communities and below-ground processes. That is, the loss of genotypic diversity represents a loss of focal genotypes, as well as the loss of the associated above- and below-ground patches of ecosystems.

(b) Linking canopy spectra, canopy chemistry and below-ground processes

Canopy spectra were correlated with foliar traits, which in turn were correlated with soil traits. The spectra that described most of the variation in foliar traits occurred in wavelength ranges known to represent variation in important physiological traits [106,114], foliar chemistry [107,108] and leaf/canopy structure. In particular, strong correlations between spectral variation and foliar variation occurred in the four AVIRIS bands between 531 and 560 nm, which includes the 531 nm wavelength associated with the

photochemical reflectance index [106,115]. Reflectance at 531 nm has been widely interpreted as an indicator of photosynthetic radiation use efficiency owing to absorption features associated with the de-epoxidation of xanthophylls during non-photochemical quenching, and more generally correlates with total pigment pools and their variation with environmental context [105]. The significant canonical correlations of foliar traits with spectra in these green wavelengths (520–560 nm) suggest that biochemical processes associated with pigments, light use and photosynthetic downregulation (i.e. plant stress) are responsible for the variation in both foliar and spectral properties of aspen clones.

The importance of green wavelengths to the spectral–foliar canonical correlations is potentially related to genetically mediated differences among Western and Great Lakes genets in pigmentation and associated responses to environmental drivers. Some of the differences between Great Lakes and Western canonical correlations in the green spectral region are likely due to environmental differences and the timing of AVIRIS acquisition. Aside from being in a drier environment than were the Great Lakes sites, the Western genets were imaged in August (compared with July), when trees were more likely to have experienced drought stress, and potentially smaller pigment pools owing to later phenology. Nonetheless, the apparent importance of wavelengths associated with pigments and xanthophyll cycle processes in discriminating among aspen genets within regions points towards significant functional differences among aspen genets, especially among genets in the west, but also broadly between Western and Great Lakes genets. This interpretation emerges from our understanding of key physiological features in imaging spectroscopy data, because we did not measure pigments or photosynthetic capacity in the field.

The strong spectra–foliar canonical correlations in wavelengths around the red edge (700–730 nm) suggest differences in photosynthetic capacity among clones. We also found strong canonical correlations between shortwave infrared wavelengths greater than 2000 nm and foliar traits. These wavelengths are closely associated with both nitrogen and ligno-cellulose compounds in vegetation, once again suggesting that spectral data captured important chemical variation relevant to both photosynthetic capacity (via nitrogen) and decomposition (via lignin).

Variation in AVIRIS spectra was correlated with variation in foliar tannin, lignin and nitrogen concentrations. Among these, condensed tannins showed the strongest canonical relationship with the spectral data. Of the foliar chemistries we measured, tannins varied the most across genets, and had the strongest correlations with canonical dimensions related to soil responses. Foliar tannins can have important below-ground functions, and are a key driver of ecosystem variation in *Populus* systems [61]. For instance, tannins typically retard decomposition and nitrogen cycling in soils as a consequence of their protein-binding capabilities and phenol active groups [55]. Intraspecific variation in tannin production affects various below-ground processes such as nitrogen mineralization [61] and decomposition [14]. As an emergent property of our analyses, these results strongly suggest the capacity to map variation in foliar condensed tannins, and the below-ground consequences thereof, at least in aspen forests.

Canopy spectra were more strongly related to variation in soil processes than were field-measured foliar traits; as evidenced by canonical correlation coefficients (figure 2). Our multivariate analyses linking imagery to soils yielded strong correlations, because these analyses included all variation in canopy spectra, and were thus not limited to the variation in spectra associated with leaf nitrogen, carbon, tannin and/or lignin. These results indicate that the spectral properties of the canopy can provide more information about below-ground processes than do the suite of canopy chemistry metrics that we physically measured. For instance, variation in moisture almost certainly played an important role in driving regional variation in below-ground processes. While we did not measure soil or canopy moisture in the field, the imaging spectroscopy data we used includes bands commonly used for water index calculations (i.e. 899 and 967 nm for WBI). In addition, spectral bands in the SWIR (especially 2000–2500 nm) are also associated with water content in addition to nitrogen and ligno-cellulose. In short, canopy spectra can provide more biologically relevant information than we are able to acquire through commonly used analytical techniques by capturing variation driven by both climate and biota. Spectroscopy provides the opportunity to characterize important sources of variation in foliar traits related to chemistry without having to measure the entire range of foliar constituents. Our results provide the basis for additional studies to use spectroscopy to identify additional foliar constituents that may vary among aspen clones.

The linkage between imaging spectroscopy and field-measured variability among genotypes in foliar and soil traits may also point to the sensitivity of optical measurements to canopy architecture [116]. Although our field sampling was restricted to closed-canopy aspen stands, to the extent that there are gaps in the canopy or varying crown diameters, the imaging spectroscopy data may be sensitive to soil reflectance and moisture, especially in SWIR wavelengths greater than 1500 nm, or variable crown shading due to crown size. Inherent in the spectral data, then, is some sensitivity to features such as radiation environment unrelated to foliar chemistry that may also affect soil microbial communities.

(c) Spectral characterization of genotypic identity and genetic variation

Spectra have been used to estimate canopy chemistry [21,26] and species diversity [30,33,38,117] in multiple systems, with impressive accuracy. Here, we also demonstrate that AVIRIS imagery can also discriminate genotypes within species (i.e. genotypic identity). Canopy spectra were able to discriminate aspen genets with a high degree of accuracy in a natural environment, such that discrimination by spectra was more accurate than was discrimination by either canopy chemistry or below-ground traits (table 2). Spectral discrimination likely performed better than did chemical discrimination, because we measured a limited number of canopy leaf traits. For instance, tannins as measured by the *n*-butanol method represent a variety of secondary metabolites that can vary in chemical structure according to *Populus* genotype [118], none of which we characterized here. Many unmeasured chemical attributes of aspen foliage likely caused variation in spectra, which allowed spectra to discriminate aspen genotypes with nearly 80% accuracy. The successful spectral discrimination of aspen genotypes suggests that imaging spectroscopy data could be a useful tool for mapping aspen

genotypes and identifying areas of high or low genetic and chemical diversity in natural forests.

In addition to discriminating genotypes, differences in spectra increased with genetic distances between genets. Although microsatellites are generally considered to be neutral markers, differentiation based on microsatellite data can be indicative of genome-wide processes that also result in differentiation in loci coding for quantitative traits [119]. Genetic distance measures based on microsatellite data have been correlated with spatial distance in Western aspen [71], and have been shown to correlate with chemical distance in aspen systems at small spatial scales [59]. The ability of spectra to provide information regarding genetic variation within a species indicates the potential of imaging spectroscopy to assess landscape-scale biodiversity in addition to characterizing traits related to chemistry and function. The Mantel correlation between genetic and spectral variation also points to a possible evolutionary basis for spectral delineation of genets: as clones diverge genetically, so do their geometrical–optical properties.

(d) Imaging spectroscopy as proxies for biological data

Here, we demonstrate that remotely sensed forest canopy attributes can serve as a proxy measurement of both above- and below-ground processes. Above- and below-ground systems are often tightly linked, such that information about one system affords information about the other [120,121]. Because remote sensing is adept at quantifying the chemical attributes associated with functional traits of forest canopies, the optical properties of foliage and canopies also provide information regarding soil processes. For instance, most of the plant traits that explain global patterns of plant nutrient cycling rates, can be quantified via imaging spectroscopy [22], thereby linking plant functional type to plant 'optical type' (*sensu* Ustin & Gamon [22]). As functional trait-driven variation in leaf litter decomposition can exceed climate-driven variation [113], it follows that 'optical types' that are tightly linked with functional types may be strong predictors of below-ground responses. Key to our measurements of both genotypic variation and forest functioning is that these metrics were estimated by remotely sensed proxies [122]. The optical properties of forest canopies serve as surrogates for biologically relevant data (*sensu* Gamon [123]). This 'surrogacy hypothesis' suggests that a wide range of biological attributes important to biodiversity conservation and management can be accurately assessed with remotely sensed optical properties. As demonstrated by canonical correlations of spectral traits with foliar traits, and of spectra traits with soil traits (*r*-values approx. 0.80), remotely sensed data can provide more information over large spatial scales than is feasible to collect via traditional field plus laboratory methods. While remote sensing is not a direct replacement of field sampling, the ability of remote sensing platforms to assess biological phenomena at large spatial scales is unparalleled.

(e) Summary/conclusion

Genotypic variation within aspen can have important consequences for canopy chemistry and below-ground processes across large spatial scales such that aspen genotypes create spatial mosaics of genetically mediated ecosystem processes in North American forests. We used imaging spectroscopy to describe variation in the key canopy traits responsible for variation in soil processes. In addition, canopy spectra were better suited to discriminate genotypes across multiple scales, and also better suited to describe the genetic distance among genotypes, than were foliar traits. As a consequence, imaging spectroscopy has great potential to quantify aspen genotypic diversity and to describe intraspecific variation over large spatial scales and across multiple ecoregions. As imaging spectrometers become more prominent, remote sensing data are likely to be useful for estimating genetic diversity, and the consequences thereof, in mixed species systems.

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