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Special Feature: Advancing Spectral Biology to Understand Plant Diversity Across Scales

Tree diversity shapes the spectral signature of light transmittance in developing forests

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Abstract

Greater tree diversity often increases forest productivity by increasing the fraction of light captured and the effectiveness of light use at the community scale. However, light may shape forest function not only as a source of energy or a cause of stress but also as a context cue: Plant photoreceptors can detect specific wavelengths of light, and plants use this information to assess their neighborhoods and adjust their patterns of growth and allocation. These cues have been well documented in laboratory studies, but little studied in diverse forests. Here, we examined how the spectral profile of light (350–2200 nm) transmitted through canopies differs among tree communities within three diversity experiments on two continents (200 plots each planted with one to 12 tree species, amounting to roughly 10,000 trees in total), laying the

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groundwork for expectations about how diversity in forests may shape light quality with consequences for forest function. We hypothesized—and found—that the species composition and diversity of tree canopies influenced transmittance in predictable ways. Canopy transmittance—in total and in spectral regions with known biological importance—principally declined with increasing leaf area per ground area (LAI) and, in turn, LAI was influenced by the species composition and diversity of communities. For a given LAI, broadleaved angiosperm canopies tended to transmit less light with lower red-to-far-red ratios than canopies of needle-leaved gymnosperms or angiosperm-gymnosperm mixtures. Variation among communities in the transmittance of individual leaves had a minor effect on canopy transmittance in the visible portion of the spectrum but contributed beyond this range along with differences in foliage arrangement. Transmittance through mixed species canopies often deviated from expectations based on monocultures, and this was only partly explained by diversity effects on LAI, suggesting that diversity effects on transmittance also arose through shifts in the arrangement and optical properties of foliage. We posit that differences in the spectral profile of light transmitted through diverse canopies serve as a pathway by which tree diversity affects some forest ecosystem functions.

KEYWORDS
biodiversity–ecosystem function, canopy structure, IDENT, leaf optical properties, light quality cues, neighborhood interactions, photoreceptors, spectral canopy transmittance

INTRODUCTION

In closed-canopy forests, light in the range of photosynthetically active radiation (PAR; 400–700 nm) is a resource that can limit the carbon assimilation and growth of individual leaves and trees (Pacala et al., 1996; Tjoelker et al., 1995). Light can also be a stressor: When a leaf absorbs too much light—more than it can use for photosynthesis—its cells may incur photodamage, which is costly to repair and reduces photosynthetic efficiency (Kothari et al., 2021). At a stand scale, the capacity of a forest to capture light and fix carbon together explains a large portion of variation in productivity among stands (Reich, 2012). Physiological, phenological, or architectural differences among trees and species shape how completely and efficiently a forest canopy intercepts and uses light and may result in mixed-species forest stands being more productive than monospecific stands (Forrester et al., 2019; Kothari et al., 2021; Sapijanskas et al., 2014; Williams et al., 2017, 2021). Moreover, beyond light absorption by photosynthetic and photoprotective pigments, plants perceive variations in particular wavelengths of light, including in the UV-B, blue, green, red, and far-red regions (Figure 1a; Christie, 2007, De Wit et al., 2016). The spectral profile of light also shapes some forest functions. As incoming solar radiation interacts with the environment, its spectral profile is modified, capturing information about the composition of vegetation and other surfaces that are absorbing, transmitting, and reflecting light. Plants can use the resulting spectral profile to inform their strategies of competition, allocation, growth, and defense (Ballaré, 1999; Courbier & Pierik, 2019; Lee & Graham, 1986; López Pereira et al., 2017; Pierik & Ballaré, 2021; Schuman & Baldwin, 2018; Smith, 1982). These neighborhood context cues may be exploited by plants growing in the understory (Brelsford et al., 2022; Hovi & Rautiainen, 2020; Xu et al., 2023) and in different canopy layers (Zhang et al., 2021).

Light quality cues and their physiological consequences have been established in laboratory studies with model organisms (Ballaré et al., 1990; Pierik et al., 2013), and explored in crop systems (Dreccer et al., 2022; Jones, 2018) and to some extent with tree seedlings and seeds (e.g., Dechaine et al., 2009; Kwesiga & Grace, 1986; Lee et al., 1996; Morgan et al., 1983; Riikonen et al., 2016). Yet, how they play out across diversity gradients and in ecosystems with rich and complex signals—such as mixed species forests—is largely unknown.

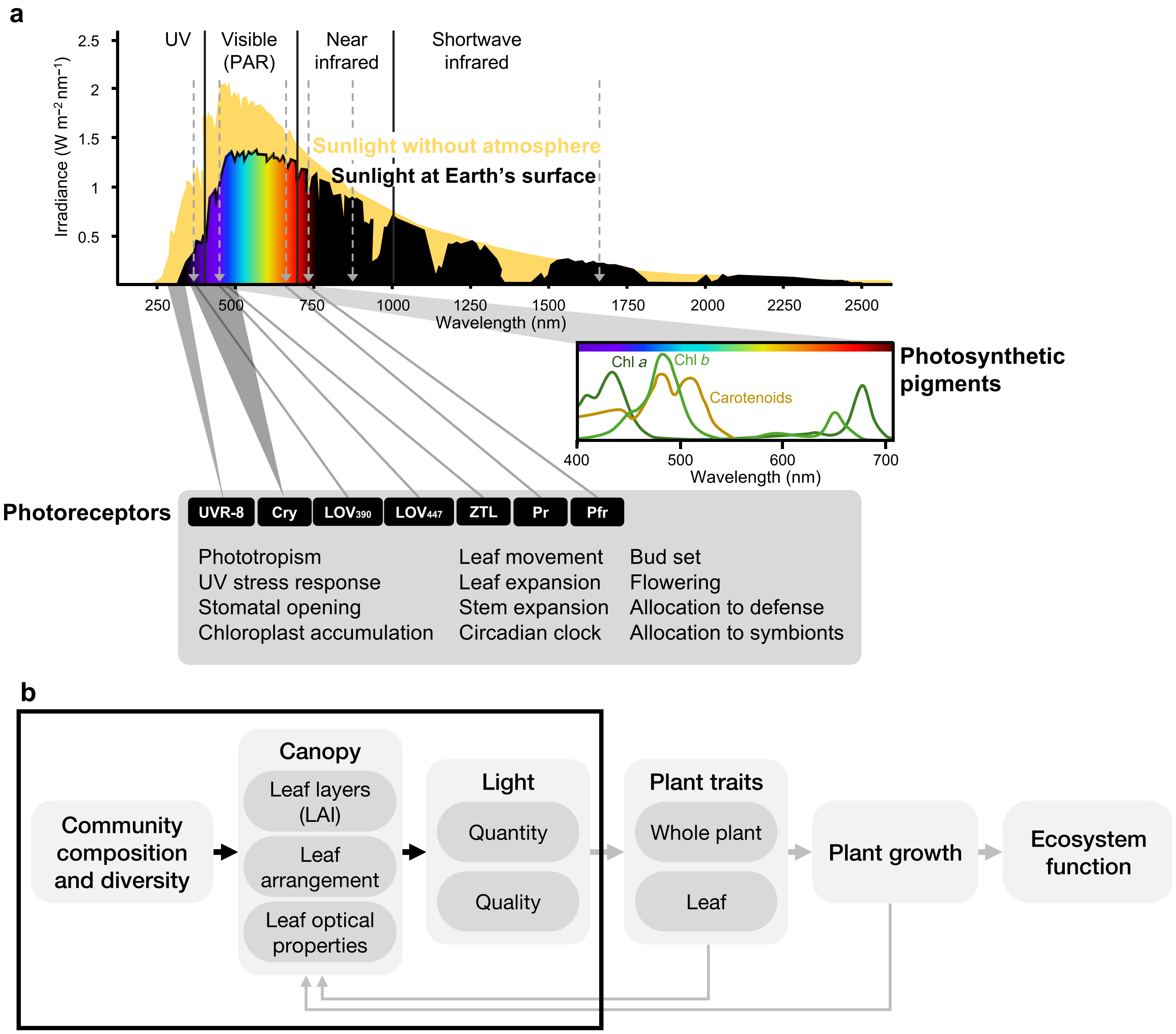

FIGURE 1 Conceptual diagram illustrating (a) biological significance of regions of solar irradiance, showing absorption spectra of select photosynthetic pigments within the region of photosynthetically active radiation (PAR, 400–700 nm) and photoreceptors with indicative functions (dashed gray arrows indicate focal wavelengths), and (b) hypothesized drivers and consequences of light quality and quantity, connecting community composition to canopy transmittance and canopy transmittance to the functioning of individual plants, plant communities, and ecosystems (black box delineates the portion examined in this study).

In theory, light-quality-mediated shifts in plant function could shape relationships between the diversity of plant communities and their productivity and trophic interactions. For instance, light quality cues indicative of competitors, such as reduced red-to-far-red ratios, may lead plants to reduce their expression of chemical defenses and preferentially allocate resources to apical growth (Ballaré, 2014; Ballaré & Pierik, 2017; De Wit et al., 2013; Izaguirre et al., 2006; Lee et al., 1996). Shifts in plant architecture in response to light quality cues (Morgan et al., 1983; Riikonen et al., 2016) could influence how crowns are positioned relative to each other in space, leading to crown complementarity and canopy packing which, in turn, are associated with forest productivity (Guillemot et al., 2020; Horn, 1971; Jucker et al., 2015; Pretzsch, 2014; Williams et al., 2017). As well as shaping the contemporaneous function of individual trees that together determine how forests function, the transmittance of light through tree canopies may also influence interactions among tree species that guide forest development and succession. The fraction, frequency, and perhaps quality of light transmitted through canopies may facilitate or inhibit the establishment of other species (Adams et al., 2007; Dechaine et al., 2009), thus shaping forest composition and function through time.

Previous work shows that overall transmittance as well as the transmittance of different wavelengths of light differs among canopies composed of different broadleaf species (Messier & Bellefleur, 1988) and between canopies composed of broadleaf and needleleaf species (Federer & Tanner, 1966; Hovi & Rautiainen, 2020; Leuchner et al., 2007; Lieffers et al., 1999; Messier & Puttonen, 1995). How much light is transmitted through crowns and canopies composed of a given species may be related to their successional status and shade tolerance (Valladares & Niinemets, 2008), with earlier successional (less shade-tolerant) tree species expected to have greater overall transmittance than later successional (more shade-tolerant) species (Canham et al., 1994; Reich et al., 2003). Moreover, canopies composed of broadleaf trees tend to transmit light with a lower red-to-far-red ratio than needleleaf canopies (Hovi & Rautiainen, 2020; Lieffers et al., 1999)—a light quality cue that is detected by plant photoreceptors and can trigger a cascade of physiological and morphological responses known as the shade avoidance syndrome (Ballaré & Pierik, 2017).

The total amount of light transmitted through canopies, as well as the relative transmittance at different wavelengths (light quality), is largely determined by the amount of foliage within the canopy (i.e., leaf area index, LAI, in square meters per square meter) (Hovi & Rautiainen, 2020; Kükenbrink et al., 2021). However, species composition may also affect canopy transmittance via leaf optical properties; that is, how much light species' leaves reflect, absorb, and transmit at different wavelengths. Cues from these subtler effects might be more important for immediate neighbors or within canopies than for the understory. Species composition may also affect the spatial arrangement of leaves, such as leaf clumping and angles, which affects gaps and how much sunlight passes directly through canopies as well as the scattering of light (Hovi & Rautiainen, 2020; Yang et al., 2023), thus affecting light quality through canopies as well.

Mixing species may alter canopy transmittance through similar pathways. Mixing species can increase LAI (Williams et al., 2021) and the spatial complementarity and packing of crowns (Jucker et al., 2015; Williams et al., 2017). Moreover, species may express different leaf trait values when growing in mixtures (e.g., Benavides et al., 2019; Felix et al., 2023; Williams et al., 2020); as for many traits, leaf optical properties display species-typical differences that track evolutionary relationships (Meireles et al., 2020), yet genetic and environmental influences also cause optical properties to vary within species (Czyż et al., 2023; Li et al., 2023).

Understanding how the spectral profile or quality of light transmitted through diverse tree canopies shapes diversity effects on ecosystem functioning requires two steps: first, understanding how diversity affects light quality, and second, how light quality affects ecosystem functioning. In this study, we take the first step: We examine how tree community composition and diversity shape the spectral profile of light transmitted through tree canopies across the ultraviolet to shortwave infrared (350–2200 nm) (Figure 1). Specifically, we focus on wavelengths known to elicit biological activity in plants (the ultraviolet, blue, red, far-red, and the red-to-far-red ratio) plus another two wavelengths to characterize the remainder of the spectrum (near infrared and shortwave infrared) (Figure 1a).

Across three tree diversity experiments located on two continents, amounting to 200 plots each planted with one to 12 tree species, we characterized the variation among tree communities in canopy transmittance as well as diversity effects (i.e., monoculture to mixture differences) on canopy transmittance. We hypothesize that the composition and diversity of tree species planted in the plots affect the spectral profile of light transmitted through their canopies via altering one or more of the three pathways outlined above (Figure 1b): LAI, the optical properties of leaves (specifically, leaf transmittance), and how leaves are arranged (from clumped to evenly dispersed). One conspicuous dimension of variation among these communities is that they include angiosperms and gymnosperms: the two major lineages of trees. We anticipate that the tendency for greater within-shoot clumping of leaves in gymnosperms than in angiosperms will result in gymnosperm canopies transmitting more direct sunlight for a given LAI—enriching the transmission of red to far-red light. Conversely, we anticipate mixed species canopies will tend to have lower overall transmittance than monocultures due to diversity-enhanced growth and LAI and will tend to display greater crown complementarity and canopy packing than monocultures, resulting in mixtures transmitting less red to far-red light. By testing these hypotheses, we aimed to reveal pathways by which tree community composition and diversity shape canopy light transmittance with potential consequences for forest function.

METHODS

Study Sites

This study was conducted across three tree diversity experiments which form part of IDENT (the International Diversity Experiment Network with Trees) (Tobner et al., 2014) and the international

TABLE 1 Details of the three tree diversity experiments within which this study was conducted.

	Experiment		
	IDENT-Cloquet	**IDENT-Freiburg**	**FAB-1**
Location (city, state if applicable, country)	Cloquet, MN, USA	Freiburg, Germany	East Bethel, MN, USA
Location (latitude, longitude)	46° 40′ 46″ N, 92° 31′ 09″ W	48° 01′ 10″ N, 7° 49′ 37″ E	45°24′17″ N, 93° 11′ 25″ W
Elevation (m a.s.l.)	382	240	282
Mean annual air temperature (°C)	4.9	11.6	6.8
Mean annual precipitation (mm)	824	881.8	777
Plot size (m)	2.8 × 2.8	3.15 × 3.15	4 × 4
Tree spacing (m)	0.4	0.45	0.5
No. trees per plot	49	49	64
Species richness levels	1, 2, 6	1, 2, 4, 6	1, 2, 5, 12
Species pool (12 species)	*Acer saccharum*, *Acer platanoides*, *Betula papyrifera*, *Betula pendula*, *Larix decidua*, *Larix laricina*, *Picea abies*, *Picea glauca*, *Pinus strobus*, *Pinus sylvestris*, *Quercus robur*, *Quercus rubra*	*Acer saccharum*, *Acer platanoides*, *Betula papyrifera*, *Betula pendula*, *Larix decidua*, *Larix laricina*, *Picea abies*, *Picea pungens* var. *glauca*, *Pinus strobus*, *Pinus sylvestris*, *Quercus robur*, *Quercus rubra*	*Acer negundo*, *Acer rubrum*, *Betula papyrifera*, *Juniperus virginiana*, *Pinus banksiana*, *Pinus resinosa*, *Pinus strobus*, *Quercus alba*, *Quercus ellipsoidalis*, *Quercus macrocarpa*, *Quercus rubra*, *Tilia americana*
Measurement window for spectra	Jul 26–30, 2021	Jul 1–7, 2021; Jul 20–22, 2021	Jul 19–23, 2021
Measurement window for LAI	Aug 13–16, 2021	Aug 19–20, 2021	Aug 18–25, 2021

Note: Mean annual air temperature and precipitation averaged over 1980–2019 at IDENT Cloquet, 1989–2019 at IDENT-Freiburg, and 1984–2018 at FAB-1.
Abbreviation: LAI, leaf area index.

network of tree diversity experiments, TreeDivNet (Paquette et al., 2018): IDENT-Cloquet (Minnesota, USA), IDENT-Freiburg (Germany), and the Forest and Biodiversity Experiment 1 (FAB-1; Minnesota, USA) (Table 1; Appendix S1: Figure S1). These experiments comprise plots (2.8 × 2.8 m to 4 × 4 m, depending on the experiment) planted with trees at high density (0.4–0.5 m spacing) in a grid pattern. The composition and species richness of planted trees are manipulated across plots: Each experiment draws from a pool of 12 temperate and/or boreal species (Appendix S1: Table S1), which include angiosperms and gymnosperms and range widely in their shade tolerance (Niinemets & Valladares, 2006). Each species is planted in plots of monoculture and various mixtures of two to 12 species. Species mixtures were designed to represent gradients of functional and phylogenetic diversity, and species were planted in nearly even proportions within mixed species plots.

We chose a set of focal plots in each experiment (Appendix S1: Table S2), including monocultures of each species as well as various mixtures of angiosperms, gymnosperms, and both angiosperms and gymnosperms. The following field measurements were taken during the peak of the growing season in July (spectral measurements) and August (leaf area index) of 2021 (Table 1). At this time, the experiments were in their 9th to 12th year and canopies were closed on most plots; the 90th percentile tree height per plot ranged from 1.3 to 12.6 m at IDENT-Cloquet, 2.3–7.9 m at IDENT-Freiburg, and 1.1–7.5 m at FAB-1.

Canopy Transmittance

Canopy transmittance, defined as the ratio of irradiance below the tree canopy to the irradiance above the tree canopy, was measured continuously at 3–8 nm spectral spacing across the electromagnetic spectrum from 350 to 2500 nm. Three measurements were taken at the same location in each focal plot—approximately at the center of the plot, below the tree canopy but above any herbaceous layer (~0.5 m above ground), and equidistant among the planted trees (Appendix S1: Figure S1). Irradiance within plots was measured with a portable spectroradiometer fitted with a cosine receptor (SVC HR-1024i; Spectra Vista Corp. Poughkeepsie, NY). Irradiance above the tree canopy was assessed by measuring incoming solar radiation in an open-sky location adjacent to each experiment with a spectroradiometer (ASD FieldSpec; Analytical Spectral Devices) fitted with a fiber optic cable pointed at a spectralon panel that was mounted and leveled on a tripod; we took the cosine of radiance to convert to irradiance. Below-canopy measurements at all sites were measured with the same SVC spectroradiometer; the open-sky measurements were taken with the same make and model of spectroradiometer across sites, but the specific instrument used differed between the sites in the USA and Germany. All spectroradiometers were radiometrically calibrated by the manufacturer.

To calculate canopy transmittance, below-canopy irradiance measurements were matched with open-sky irradiance measurements. System times on measurement computers were synced at the start of the campaign. Open-sky measurements were set to be taken as frequently as the instrument would allow (~1-s interval); 95% of measurements were matched to an open-sky measurement within 6 s; measurements on 11 of the 200 plots were matched at a longer time interval (ranging from 9 to 451 s). Spectra from the two instruments were resampled to 1 nm resolution. Canopy transmittance (T) for each wavelength (λ) was calculated as follows:

$$T(\lambda) = \frac{I_{\text{canopy}}(\lambda)}{I_{\text{ref}}(\lambda)} \times c(\lambda) \tag{1}$$

where I_{canopy} is the irradiance measured below the canopy, I_{ref} is the open-sky reference irradiance (converted from radiance) measured near-simultaneously, and c is an inter-instrument correction factor for each wavelength that accounts for measurement differences between the instruments used to measure open-sky (reference instrument) conditions and conditions below the canopy (canopy instrument). To estimate $c(\lambda)$, several simultaneous readings were taken with the two instruments side by side in open-sky conditions; this was repeated at multiple time points during each sampling day, and $c(\lambda)$ was calculated for each pair of readings as follows:

$$c(\lambda) = \frac{I_{\text{reference instrument}}(\lambda)}{I_{\text{canopy instrument}}(\lambda)} \tag{2}$$

$c(\lambda)$ values were averaged to give one value per wavelength for each time point, linearly interpolated between time points (or extrapolated as needed) to give one value per second, and time-matched to the below-canopy irradiance measurement as above (Appendix S1: Figure S2).

All measurements were taken within 3 h (±3 h) of solar noon. We calculated sun elevation for each measurement using the photobiology package (Aphalo, 2015) in R (v 4.3.0; R Core Team, 2023) and found no systematic effect of the sun elevation on canopy transmittance at any of our focal wavelengths or on the ratio of red to far-red transmittance ($\chi^2 \leq 0.94$, $\text{df} = 1$, $p \geq 0.332$). To minimize the potential influence of variable incoming light, measurements would ideally be taken under uniformly clear sky conditions. While such conditions did not occur during our sampling window, all transmittance values are expressed relative to incoming irradiance and plots were measured in random order to avoid systematic bias. The three measurements of canopy transmittance per location were visually screened to remove erroneous readings (e.g., an individual spectrum that differed markedly from the other measurements at a location) and averaged to give one value for each plot. Spectral regions with especially low signal-to-noise were removed (namely, 1350–1450 nm and 1800–1980 nm, because these regions are affected by atmospheric water vapor which absorbs solar radiation, and 2200–2500 nm, because cosine receptors have low sensitivity above 2200 nm) (Hovi & Rautiainen, 2020). Canopy transmittance was examined specifically in the ultraviolet (the spectral band centered at 360 nm, T_{UV}), blue (440 nm, T_{B}), red (660 nm, T_{R}), far-red (730 nm, T_{FR}), and PAR (400–700 nm, T_{PAR}), and for the red-to-far-red ratio (660 nm/730 nm, $T_{\text{R:FR}}$)—as known regions of biological importance—as well as in the near infrared (865 nm, T_{NIR}) and shortwave infrared (1615 nm, T_{SWIR}). Note that the transmittance spectra for some plots remain noisy (see, e.g., Figure 2c) due to imperfect spatio-temporal matching between the open-sky and below-canopy measurements; while we could dampen such noise by applying a statistical filter, our focal spectral regions appeared stable and would be minimally affected by filtering; thus, we show and analyze unfiltered spectra.

Leaf Area Index

LAI, the one-sided projected area of leaves per area of ground (in square meters per square meter), was estimated with an LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebraska). This instrument consists of two wands, each with an optical sensor that detects radiation in the blue range (320–490 nm, where leaves are assumed to absorb all radiation) across five viewing angles. The instrument captures the contrast

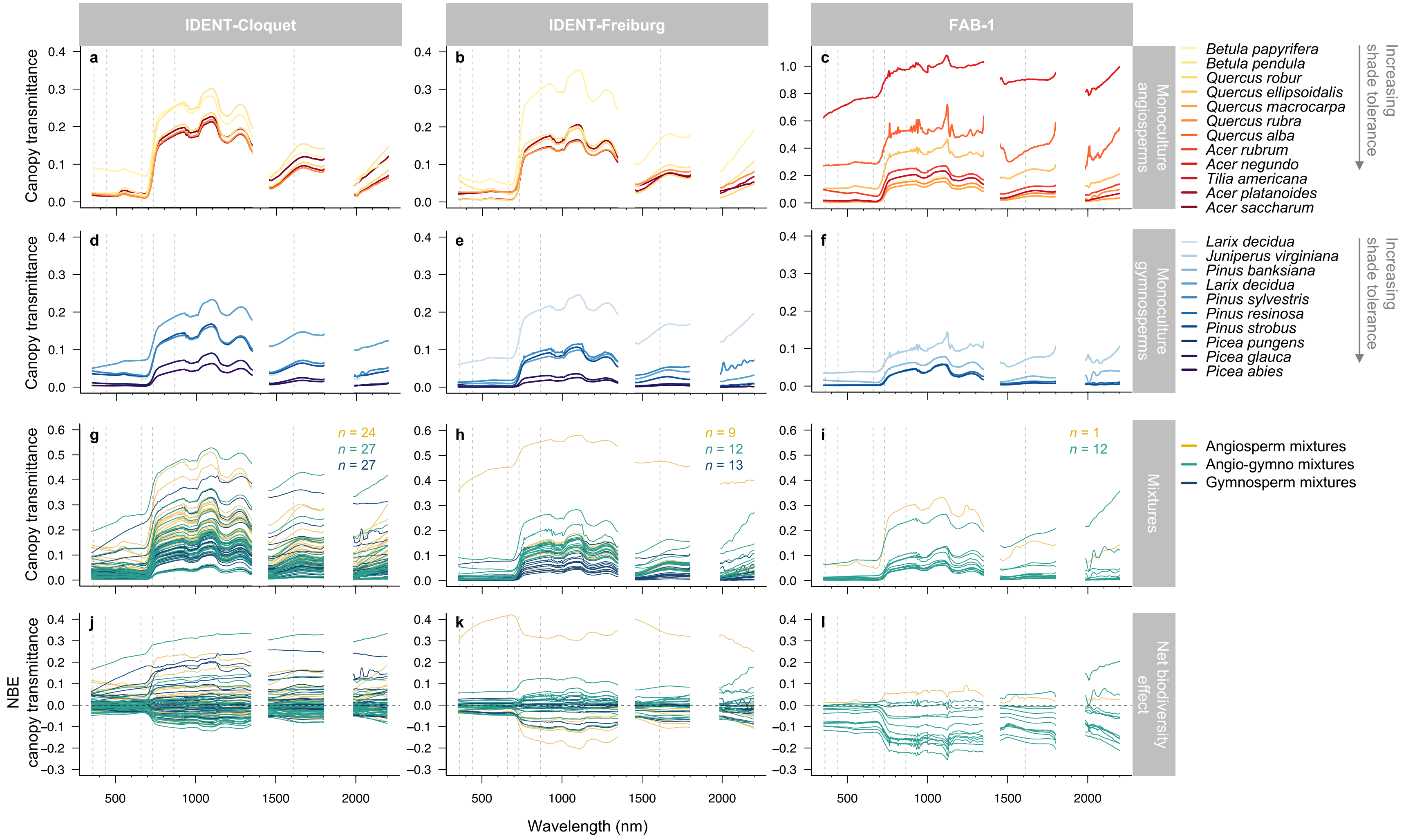

FIGURE 2 Full-range (350–2200 nm) canopy transmittance in monocultures and species mixtures, and the net biodiversity effect (NBE) on canopy transmittance at the three tree diversity experiments (IDENT-Cloquet, IDENT-Freiburg, and FAB-1). Mean canopy transmittance of (a–c) angiosperm monocultures and (d–f) gymnosperm monocultures; color-coded by species' shade tolerance (Appendix S1: Table S1, Niinemets & Valladares, 2006). (g–i) Canopy transmittance of each mixed-species plot; color-coded by lineage composition (*n* indicates the number of plots). (j–l) NBE on canopy transmittance (i.e., observed in species mixtures minus expected, based on the same species in monoculture). Especially noisy spectral regions have been removed. Dashed gray lines indicate focal wavelengths.

between the canopy and sky to estimate gap fraction by viewing angle ($G(\theta)$), from which transmittance and LAI can be estimated as follows (Fassnacht et al., 1994; LI-COR, 1992):

$$\mathrm{LAI} = -2\int_0^{\pi/2} \ln(G(\theta)) \cos\theta \sin\theta \, d\theta \quad (3)$$

At each site, the two wands were cross-calibrated according to manufacturer instructions, and one was positioned in an open area adjacent to the experiment and set to log at 15-s intervals while measurements were taken below the canopy on forest plots. Measurements were taken in diffuse light conditions (overcast, dawn or dusk). To account for spatial variability in canopy structure, one to three measurements were taken at 0.5 m above ground (matching the height of the canopy transmittance measurements) at each of four (IDENT-Cloquet and IDENT-Freiburg) or five (FAB-1) locations in the center of plots (Appendix S1: Figure S1).

The LAI-2000 underestimates the LAI of conifers because conifer needles are clumped together in shoots (Gower & Norman, 1991). To account for within-shoot clumping, we multiplied the LAI-2000 measurements by correction factors that capture the area of needles within a shoot and the projected area of the shoot, accounting for the fact that the shoot can be oriented in any direction (following the approach of previous studies, including Chen et al., 2006; Majasalmi et al., 2013; Stenberg, 1996). We applied the following correction factors: 1.42 for *Larix laricina* and *Larix decidua* (Sonnentag et al., 2007), 1.553 for *Picea abies*, *Picea glauca*, and *Picea pungens* (Stenberg et al., 1995), 1.91 for *Pinus strobus* (Chen et al., 2006), 1.42 for *Pinus banksiana* (Chen et al., 2006), 1.80 for *Pinus resinosa* (Fassnacht et al., 1994), and 1.701 for *Pinus sylvestris* (Smolander et al., 1994). In mixed-species plots, we considered the LAI per species to be proportional to the live basal area per species (Appendix S1: Figure S3) and applied correction factors accordingly. LAI for broadleaf species and *Juniperus* was not modified. To assess the influence of within-shoot clumping, we compared estimates of LAI with clumping corrections (i.e., our best estimate of true LAI, hereafter "LAI") to those without corrections (termed $\mathrm{LAI}_{\mathrm{effective}}$); we use the term "effective" in the sense of effectiveness in intercepting light.

Canopy transmittance and LAI were also measured in the same fashion on all plots at ~2 m above ground, to give a measurement of transmittance and overlying LAI partway through canopies (results reported in Appendix S2). We applied correction factors for LAI using the same species proportions as for the below-canopy measurements, which undoubtedly introduce error given that species (and thus their crowns) differ in height.

Individual Leaf Transmittance

For each species at each site, we collected leaves and measured their optical properties. For one tree per species in monoculture, leaves were collected from each of three crown heights: top (within 30 cm of the top of the crown), middle (midway between the top and bottom of the crown), and base (within 30 cm of the bottom of the crown). There were two exceptions: Due to the small size of trees and high mortality, respectively, *Acer negundo* at FAB-1 was sampled in the 12-species mixture (and only a top-of-crown leaf was sampled) and *Betula papyrifera* at Freiburg was sampled from the six-species mixture of North American species. Leaves were selected to be fully expanded, from the current year's growth (of relevance to the evergreen species which may retain multiple cohorts of leaves), and representative of the condition of leaves in the tree's crown.

Leaf transmittance was measured with an integrating sphere (DC-R/T, Spectra Vista Corp. Poughkeepsie, NY) attached to a spectroradiometer (SVC HR-1024i; Spectra Vista Corp. Poughkeepsie, NY). We followed the protocol of Laliberté and Soffer (2018a) for broadleaf species and Laliberté and Soffer (2018b) with modifications for needle-leaf species. In brief, a sample of needles was spaced 0.5–1 needle-width apart in a single layer within carriers (Hovi et al., 2020). The gaps among needles result in less light being reflected (gaps do not reflect any light) and more light being transmitted (gaps transmit all light) than if the leaf were wide enough to cover the entire opening of the sample port on the integrating sphere. This approach provides a standardized single layer of needles by standardizing rather than eliminating naturally occurring gaps and avoiding multiple scattering among needles. To normalize measurements of optical properties to the proportion of area covered by needles, we then assumed there was no transmittance through needles at 400 nm following Noda et al. (2013) and calculated a gap fraction (g) for each sample of needle leaves (i) as follows:

$$g_i = \frac{T_{\mathrm{tar400},i}}{T_{\mathrm{ref400},i}} \quad (4)$$

where $T_{\mathrm{tar400},i}$ is the target radiance for leaf i at 400 nm in transmittance mode and $T_{\mathrm{ref400},i}$ is the reference radiance for leaf i at 400 nm in transmittance mode. We used g to correct transmittance (τ) for each leaf sample (following Laliberté & Soffer, 2018b; Noda et al., 2013), as follows:

$$\tau_i = \left(\frac{T_{\text{tar},i}}{T_{\text{ref},i}} - g_i\right) \times \left(\frac{1}{(1-g_i)}\right) \quad (5)$$

For input into linear models (see below), we used leaf transmittance values to calculate community-weighted mean (CWM) values of leaf interception. Leaf transmittance was averaged across the top, middle, and bottom canopy leaves to give one mean value per species. For each plot, the CWM leaf transmittance was calculated by weighting the leaf transmittance of each species by the relative basal area of that species on the plot; that is, assuming LAI per species to be proportional to the live basal area per species (Appendix S1: Figure S3). Values were expressed as leaf interception (1 − τ) such that values are consistent in direction with LAI; that is, increasing values imply increasing interception of light. In addition, to assess the effect of within-community variation in leaf transmittance, we calculated functional dispersion (FDis) of leaf transmittance for each plot using the FD package in R (Laliberté et al., 2014; Laliberté & Legendre, 2010); we used the mean leaf transmittance values for each species weighted by their relative basal area on the plot.

Net Biodiversity Effects

The net biodiversity effect (NBE) on canopy transmittance was calculated on each mixed species plot as the canopy transmittance observed in the mixed species plot minus the weighted mean of the canopy transmittance of those same species in monoculture (weights were the proportion of each species planted in mixture; following Loreau & Hector, 2001). Where more than one monoculture plot was measured for a species at a site, the monoculture canopy transmittance was averaged across these plots. The same approach was used to calculate the NBE on LAI.

Statistical Analyses

Data preparation and statistical analyses were conducted in R (v 4.3.0; R Core Team, 2023). To examine drivers of canopy transmittance and the NBE on canopy transmittance, mixed effects models were fitted using the nlme package (Pinheiro & Bates, 2023); this approach allows us to account for the spatial structure in our data by treating Site as a random effect. A series of models were fitted with canopy transmittance at a select wavelength or ratio of wavelengths as the response variable. LAI, lineage composition (whether the tree community was composed of angiosperms, gymnosperms, or mixtures of the two), the community-weighted mean leaf interception at the corresponding wavelength (or ratio), and interactions between LAI and lineage composition were predictor variables. Models were also fitted for the NBE on canopy transmittance at each of the same wavelengths or ratios of wavelengths, with the NBE on LAI, lineage composition, and their interactions as predictor variables. Canopy transmittance values were $\log_{10}$ transformed before analysis to improve normality. Likelihood ratio tests, comparing models with and without a given term, were used to test the significance of terms within models. Parameter estimates were taken from models fitted with restricted maximum likelihood. As a measure of the goodness of fit of models, the marginal coefficient of determination for fixed effects (R_m^2) was calculated with the MuMIn package (Barton, 2023). For each lineage composition, squared Pearson's correlation coefficients were calculated between the observed values and values predicted from the population-level (fixed effects) model. The independent contribution of each predictor variable to canopy transmittance was calculated for an additive model (with random effects) using hierarchical partitioning implemented in the glmm.hp package (Lai et al., 2022). For simplicity, we took a straightforward statistical approach in our analyses, but a fruitful extension would be to use an approach grounded in physics; for instance, structuring analyses following the Beer–Lambert law, and/or using radiative transfer models (e.g., Gastellu-Etchegorry et al., 1996; Hovi et al., 2024; Kükenbrink et al., 2021; Plekhanova et al., 2021) to formulate hypotheses to test with empirical data.

RESULTS

Canopy Transmittance Among Tree Communities

Canopies composed of different species had different transmittance signatures (Figure 2a–f). Single-species canopies composed of more shade-tolerant species tended to transmit less light throughout the spectrum than canopies of shade-intolerant species, with some differences evident within the visible region and especially evident at wavelengths beyond this region. The relationship between species' shade tolerance and total canopy transmittance was especially evident among gymnosperm species (Pearson's correlations −0.79, −0.79, and −0.68 at Cloquet, Freiburg, and FAB-1, respectively; Figure 2d–f). Across all species, a negative correlation between canopy transmittance and species shade tolerance was evident at Cloquet and Freiburg

(Pearson's correlations −0.50 and −0.54, respectively), but not at FAB-1 (0.38). Considerable variation in canopy transmittance was observed among mixed species plots (Figure 2g–i). On average, mixed-species canopies composed of angiosperms tended to transmit more light than those composed of mixtures of gymnosperm species, with mixed angiosperm-gymnosperm canopies intermediate in transmittance (Figure 2g–i).

The transmittance of mixed-species canopies differed from expectations based on monocultures (i.e., the net biodiversity effect on canopy transmittance deviated from zero) (Figure 2j–l). Across all sites, the canopies of 55% of the mixed-species angiosperm plots, 53% of the mixed-species gymnosperm plots, and 63% of the mixed-species angiosperm-gymnosperm plots transmitted less light than expected (i.e., on average across the spectrum). These diversity effects on transmittance were especially pronounced through the near-infrared and shortwave infrared.

Community Composition and the Spectral Quality of Light Transmitted for a Given T_{PAR}

The ratio of red to far-red light transmitted through canopies ($T_{R:FR}$) was closely related to the fraction of photosynthetically active radiation transmitted through canopies (T_{PAR}) ($R^2 = 0.83$) (Figure 3). However, for a given T_{PAR}, $T_{R:FR}$ differed among communities. Notably, the relationship depended on whether canopies were composed of angiosperms, gymnosperms, or mixtures of the two ($\chi^2 = 5.98$, $df = 2$, $p < 0.001$): $T_{R:FR}$ declined more rapidly with declining T_{PAR} in angiosperm canopies than in canopies composed of mixtures of angiosperms and gymnosperms or gymnosperms (Figure 3). These compositional effects were driven by differences in T_{FR} rather than T_R (Figure 3b,c).

Drivers of Canopy Transmittance in Biologically Significant Wavelengths

Together, LAI, lineage composition, and leaf transmittance explained a large portion of observed variation in canopy transmittance across the six focal spectral regions ($R_m^2 = 0.57–0.68$; Figure 4a–f, Table 2). LAI alone explained 46%–52% of the observed variation among plots in canopy transmittance at each focal region (i.e., based upon hierarchical partitioning of the variation explained by additive models; Figure 4 insets, Appendix S1: Table S3).

The decline in transmittance with increasing LAI significantly differed with the lineage composition of canopies in the UV, blue, red, and far-red ($\chi^2 \geq 4.21$, $df = 2$, $p \leq 0.016$); significant differences were not detected in the near infrared or shortwave infrared ($\chi^2 \leq 2.78$, $df = 2$, $p \geq 0.136$). For a given LAI, angiosperm canopies tended to transmit less light than mixtures of angiosperms and gymnosperms, and gymnosperms transmitted the most (lineage composition explained 6%–11% of the variation among plots in an additive model; Figure 4 insets, Appendix S1: Table S3). These effects of lineage composition depended on within-shoot clumping; they were not observed for relationships between transmittance in any focal wavelength and $LAI_{effective}$ (i.e., LAI not accounting for within-shoot clumping; Appendix S1: Figure S4, Table S4).

Individual leaves of each species had different transmittance spectra (Appendix S1: Figure S5). However, the differences among communities in leaf transmittance (i.e., the CWM of leaf transmittance) explained only a small portion (1%–9%) of the variation observed among plots in canopy transmittance at each focal wavelength (Figure 4 insets; Appendix S1: Table S3). The magnitude of variation in leaf transmittance among species and communities was negligible relative to the variation in canopy transmittance through the UV and visible portions of the spectrum but substantial in the near and shortwave infrared (Appendix S1: Figure S5).

$T_{R:FR}$ declined with LAI (Figure 4g, Table 2), but LAI explained only 16% of the observed variation in $T_{R:FR}$ among communities. An additional 15% of variation was explained by lineage composition, and <1% by the CWM of leaf transmittance (Figure 4g inset, Appendix S1: Table S3). $T_{R:FR}$ declined more rapidly with increasing LAI in angiosperm canopies compared with mixed angiosperm-gymnosperm and gymnosperm canopies ($\chi^2 = 5.45$, $df = 2$, $p < 0.001$). These lineage differences also depended upon within-shoot clumping: While trends remained, significant differences among lineages were not evident in the relationship between $T_{R:FR}$ and $LAI_{effective}$ (Appendix S1: Figure S4g, Table S4).

While CWMs indicate the effect of dominant species, FDis indicates the effect of species' dissimilarity. Here, we can only approximate FDis from measurements made in monocultures, which likely underestimates the true value. We found that using FDis leaf transmittance in place of CWM leaf interception in our models had little effect on overall model fit (R_m^2 was unchanged for each wavelength except the red-to-far-red ratio, which was improved by 0.01). Comparing the FDis and CWM models with the Akaike information criterion (AIC) showed no difference between models in explaining transmittance in the blue, red, far red, and near infrared, but the FDis models better explained canopy transmittance in the UV, SWIR, and red to far red

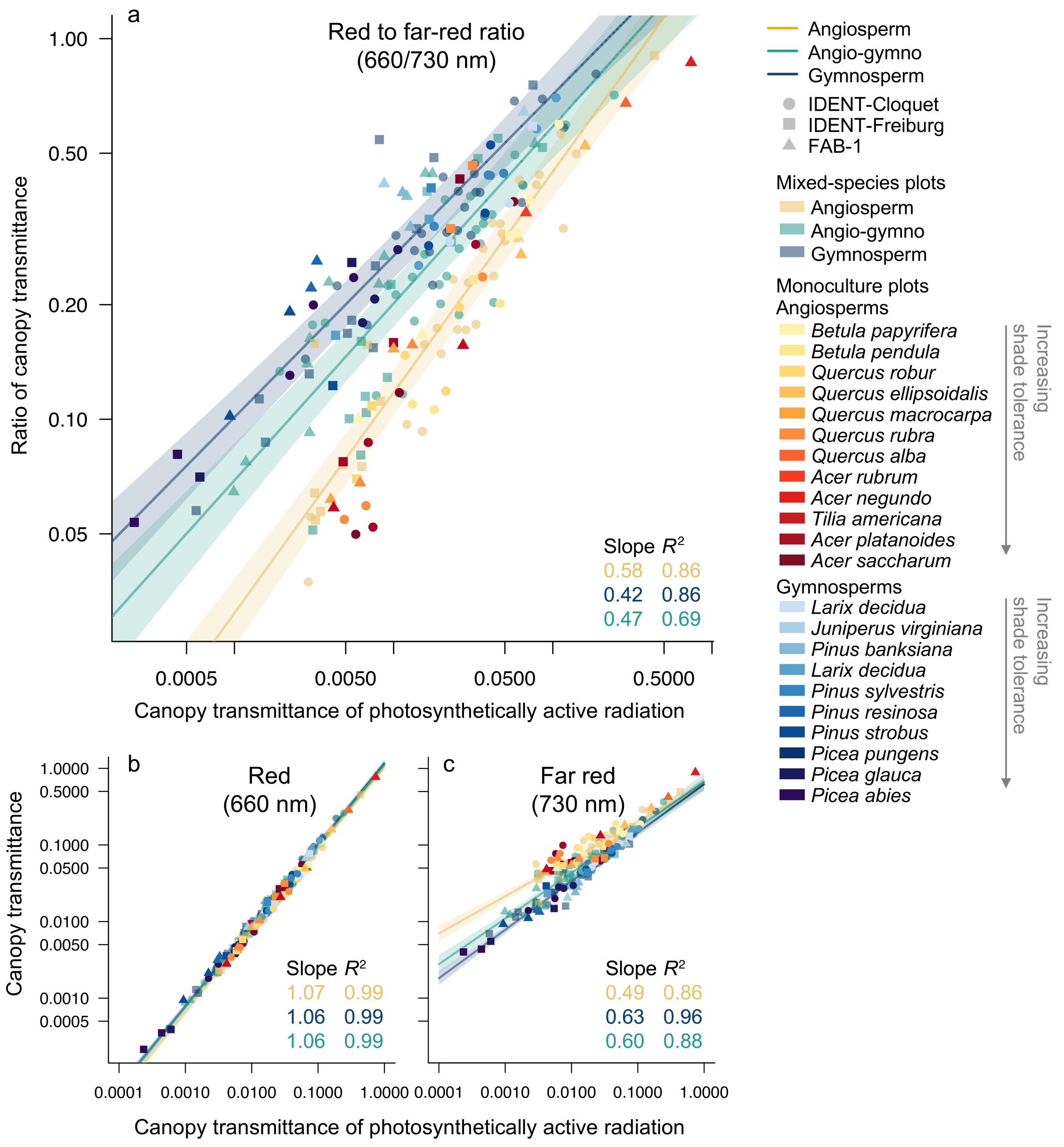

FIGURE 3 Canopy transmittance of photosynthetically active radiation and (a) the ratio of red to far-red canopy transmittance, (b) canopy transmittance in red (660 nm), and (c) canopy transmittance in the far-red (730 nm) on plots of differing composition. Squared Pearson's correlations (R^2) are shown for plots composed of each lineage (angiosperms, gymnosperms and mixtures of angiosperms and gymnosperms); shading around regression lines indicates the 95% CI. Slopes significantly differ with lineage composition in the red-to-far-red ratio ($\chi^2 = 5.98$, df $= 2$, $p < 0.01$) and far-red ($\chi^2 = 6.44$, df $= 2$, $p < 0.001$), but not red ($\chi^2 = 0.26$, df $= 2$, $p = 0.646$). Note the axes are $\log_{10}$ transformed. Monoculture plots color-coded by shade tolerance (Niinemets & Valladares, 2006).

(ΔAIC > 2, Appendix S1: Table S5). According to simulations conducted by Plekhanova et al. (2021), FDis may alter canopy transmittance by affecting light scattering.

Diversity Effects on Canopy Transmittance

Net biodiversity effects (NBEs) on $T_{\mathrm{R:FR}}$ were positively associated with NBE on T_{PAR} but showed

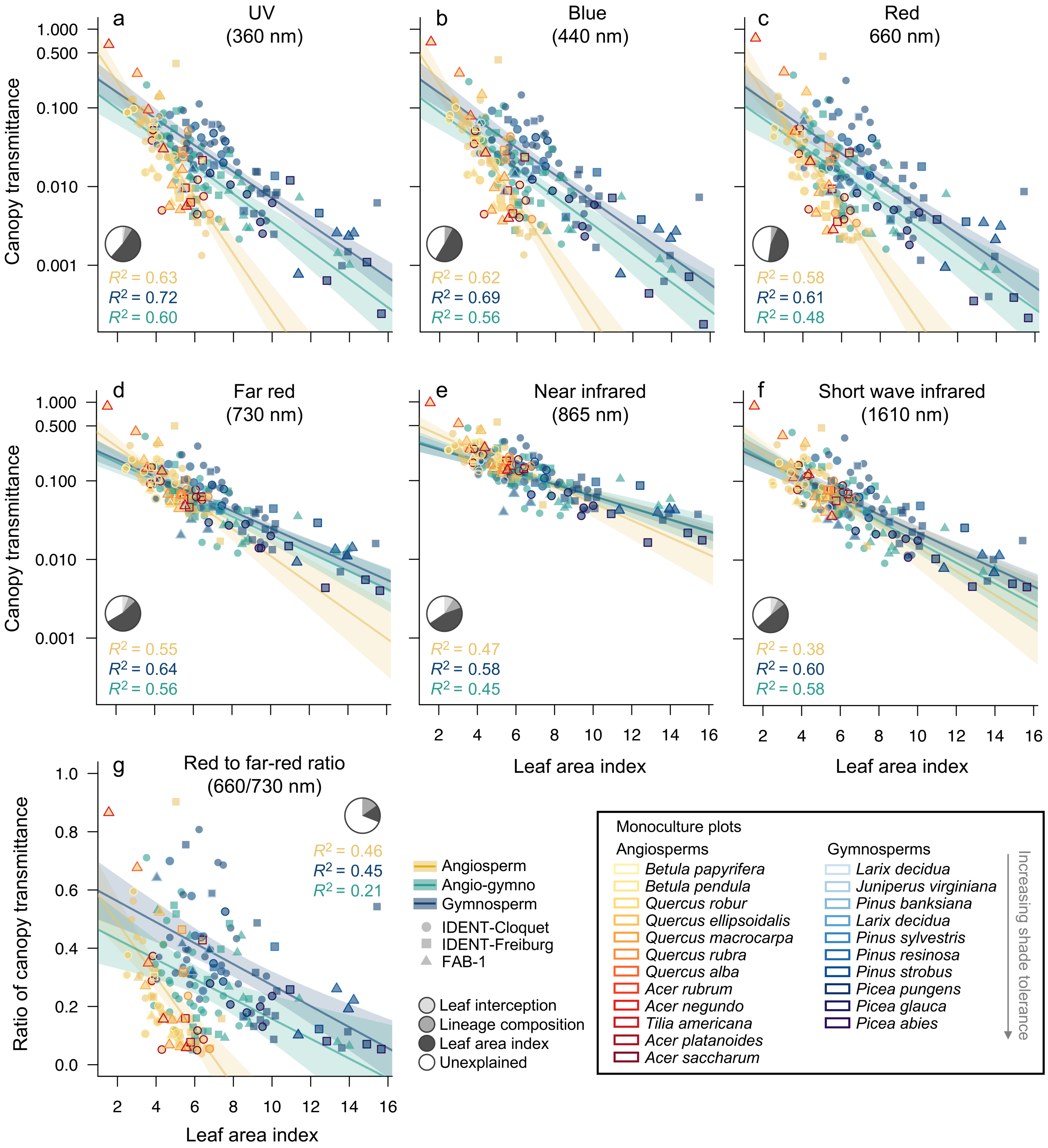

FIGURE 4 Relationship between leaf area index (LAI) and canopy transmittance at select wavelengths for plots of differing composition. Squared Pearson's correlations (R^2) among plots of each lineage composition are shown; shading around regression lines indicates the 95% CI. Note the *y*-axis of (a–f) are $\log_{10}$ transformed. Inset pie charts show the independent proportion of variation explained by each predictor (LAI, individual leaf light interception, and lineage composition) in an additive model. Slopes significantly differ with lineage composition in the UV, blue, red, far-red, and red to far-red ($\chi^2 \geq 4.21$, df = 2, $p \leq 0.016$) but not near infrared or shortwave infrared ($\chi^2 \leq 2.77$, df = 2, $p \geq 0.136$).

considerable variation for a given NBE on T_{PAR} ($R_m^2 = 0.63$; Figure 5). In each focal spectral region, more than half (58%) of mixed-species plots intercepted more light than expected from monocultures (Figure 6a–f). The NBE on LAI was significantly associated with the NBE on canopy transmittance in

TABLE 2 Coefficients and the significance of terms in mixed-effects models examining canopy transmittance in a variety of wavelengths.

Source	UV	Blue	Red	Far red	Near infrared	Shortwave infrared	Red-to-far-red ratio
Intercept	−0.918	6.326	1.618	0.006	0.031	−0.125	0.98*
LAI	−0.365***	−0.373***	−0.360***	−0.172***	−0.109***	−0.154***	−0.090***
Gymno	−0.535*	−0.523*	−0.449^{+}	−0.256^{+}	−0.197^{+}	−0.124	−0.040
Angio-gymno	−0.710**	−0.714**	−0.688**	−0.295*	−0.213^{+}	−0.112	−0.170^{+}
Leaf interception	0.986	−6.372	−1.781	−0.362	−0.437	−0.333	−0.330
LAI × gymno	0.197***	0.204***	0.193***	0.065**	0.035*	0.040	0.060***
LAI × angio-gymno	0.184***	0.191***	0.188***	0.058*	0.034^{+}	0.024	0.060***
R_m^2	0.67	0.64	0.57	0.68	0.66	0.64	0.36
R_c^2	0.67	0.64	0.57	0.68	0.66	0.65	0.38

Note: Canopy transmittance values were $\log_{10}$ transformed prior to analysis (except for the red-to-far-red ratio of transmittance). Site was treated as a random effect. Leaf interception = individual leaf light interception at focal wavelength (i.e., 1 − leaf transmittance), gymno = assemblages of gymnosperm species, angio-gymno = assemblages of angiosperms and gymnosperm species (the intercept represents assemblages of angiosperm species).

Abbreviations: LAI, leaf area index; R_c^2, conditional coefficient of determination for fixed and random effects; R_m^2, marginal coefficient of determination for fixed effects.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; $^{+}p < 0.1$.

the UV and marginally so in the near infrared (Figure 6a–f, Table 3), indicating mixed-species canopies that had more leaves than expected transmitted less light than expected in these spectral regions. These relationships did not differ with lineage composition ($\chi^2 \leq 2.96$, $\mathrm{df} = 2$, $p > 0.11$) unless within-shoot clumping was ignored: The relationship between NBE on $\mathrm{LAI}_{\mathrm{effective}}$ and NBE on transmittance in the far-red, near infrared, and shortwave infrared regions significantly differed with lineage composition ($\chi^2 \geq 4.01$, $\mathrm{df} = 2$, $p \leq 0.024$; Appendix S1: Figure S6, Table S6). Overall, a substantial portion of variation in the NBE on canopy transmittance remained unexplained by these predictors: The NBE on LAI and lineage composition together explained 26% or less of the observed variation among plots in the NBE on canopy transmittance ($R_m^2 = 0.11$–0.26; Table 3).

On nearly two-thirds (64%) of the mixed species plots, a lower $\mathrm{T}_{\mathrm{R:FR}}$ was observed than expected based on monocultures. Across all plots, less red to far-red light was transmitted than expected when canopies had higher LAI than expected; that is, the NBE on $\mathrm{T}_{\mathrm{R:FR}}$ significantly declined as the NBE on LAI increased (Figure 6g, Table 3). $\mathrm{T}_{\mathrm{R:FR}}$ tended to respond more to diversity-enhanced LAI when canopies were composed of angiosperms, but the relationship did not significantly differ with the lineage composition of the canopies ($\chi^2 = 2.96$, $\mathrm{df} = 2$, $p = 0.112$; regardless of whether within shoot clumping was considered, Appendix S1: Figure S6g, Table S6) and 89% of the variation among communities in $\mathrm{T}_{\mathrm{R:FR}}$ was not explained by these predictors ($R_m^2 = 0.11$).

DISCUSSION

Here, we found that developing forest canopies that vary in tree composition and diversity differ not only in the amount of light they transmit—in total and in the photosynthetically active range (PAR)—but also in the spectral composition of that light, including in regions that plants are known to sense. LAI, the lineage composition of forest mixtures, and leaf-level transmittance explained between 36% and 68% of the variation in spectral quality and quantity. While several previous studies have shown that the amount of PAR transmitted through canopies differs among forest communities (e.g., Duarte et al., 2021; Forrester et al., 2019; Williams et al., 2021), the influence of forest diversity on the spectral properties of transmitted light has not been systematically tested. Our findings from three tree diversity experiments on two continents confirm expectations from previous studies that LAI and forest composition are dominant drivers of canopy transmittance (e.g., Federer & Tanner, 1966; Hovi & Rautiainen, 2020), but we further show that these drivers apply across a broad spectral range for a large number of species and a diverse set of developing forest communities. Moreover, we found the transmittance of mixed-species canopies differed from expectations based on monocultures—that is, diversity effects were apparent—including for red and far-red wavelengths important for neighbor sensing and shade avoidance. We attribute these diversity effects to differences in LAI among communities and secondarily to the interaction of leaf optical properties with canopy architecture.

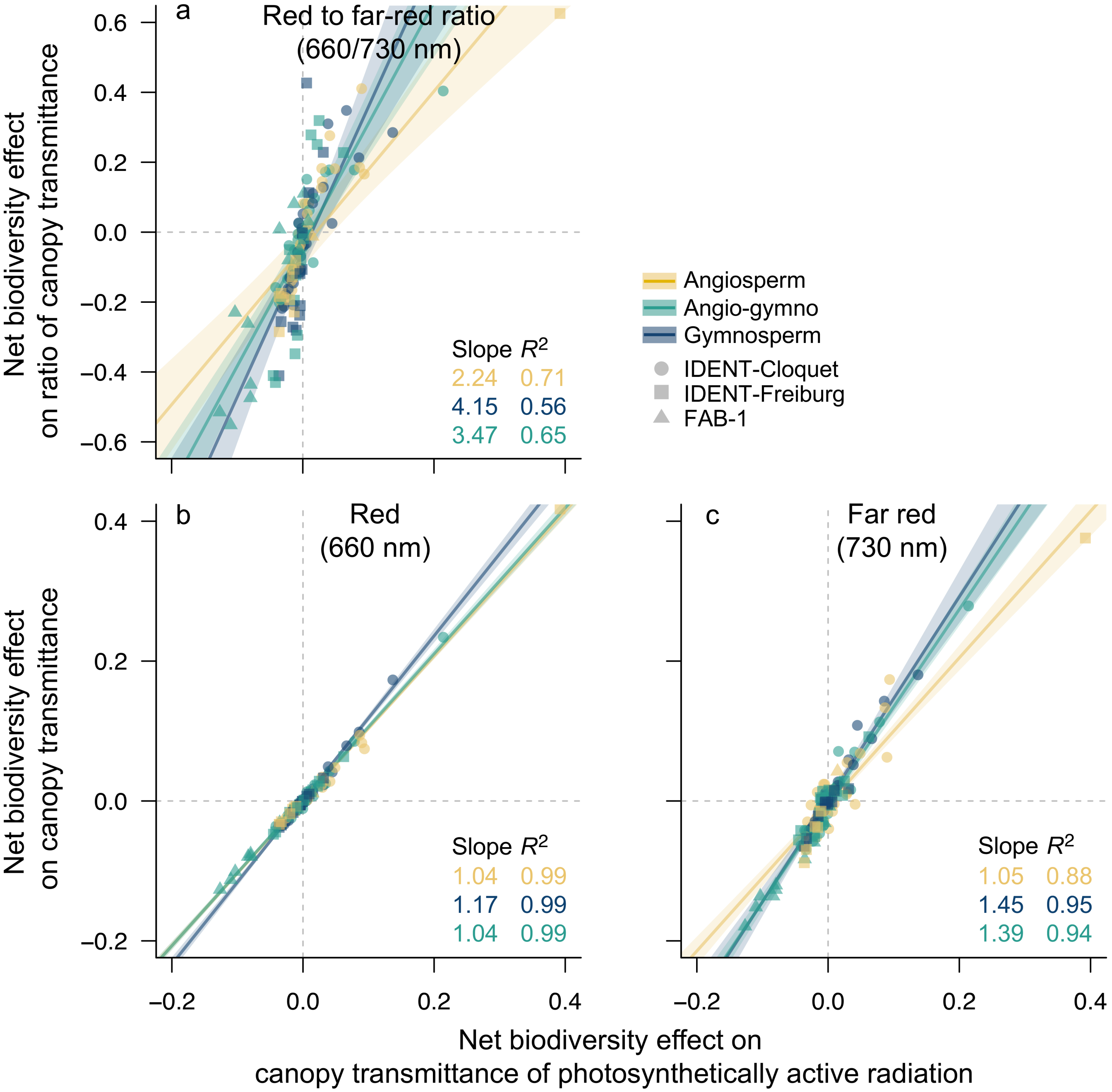

FIGURE 5 Net biodiversity effect (NBE) on canopy transmittance of photosynthetically active radiation and corresponding NBEs on (a) red to far-red canopy transmittance, (b) canopy transmittance in red (660 nm), and (c) canopy transmittance in the far-red (730 nm) on plots of differing composition. Separate slopes and squared Pearson's correlations (R^2) are shown for plots of each lineage composition ($\chi^2 \geq 5.07$, df = 2, $p \leq 0.002$); shading around the regression line indicates a 95% CI.

Radiative transfer modeling shows that the profiles of light extinction through canopies may vary with the diversity and composition of communities (Kükenbrink et al., 2021). While we focus on the spectral properties of light reaching the understory, we also measured light quantity and quality within canopies and found the effects of LAI, lineage composition, and leaf-level transmittance on canopy transmittance were broadly consistent both within and beneath canopies (Appendix S2).

Community Composition Affects Canopy Transmittance in Biologically Important Wavelengths via LAI, Canopy Structure, and Leaf Optical Properties

By shaping both the light quantity and quality, canopy transmittance may drive forest succession by limiting which species can recruit and grow. Previous work suggests that canopy transmittance in mature forests with similar basal areas may decline with species' shade

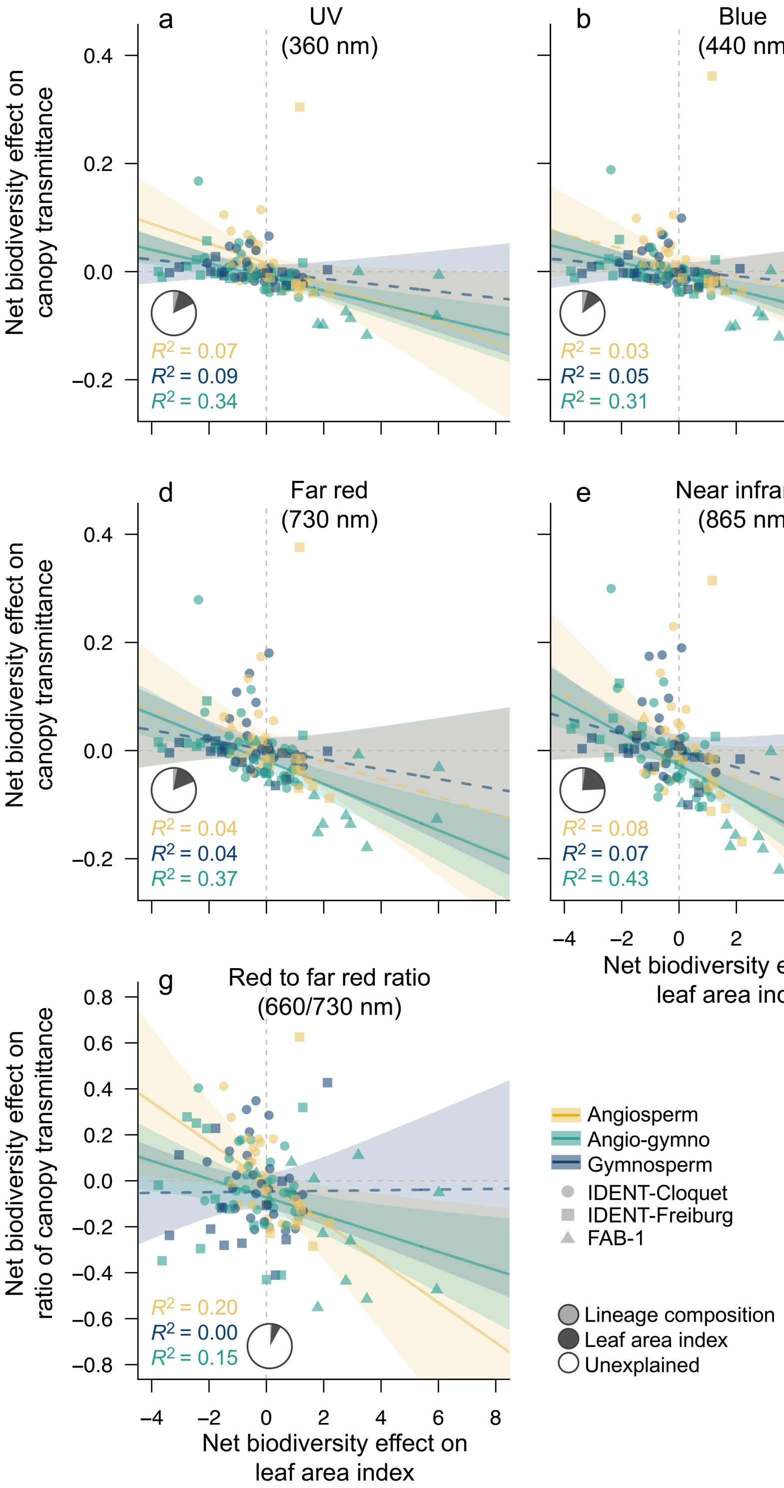

FIGURE 6 Relationship between the net biodiversity effect (NBE) on leaf area index (LAI) and the NBE on canopy transmittance at select wavelengths for plots of differing composition. Squared Pearson's correlations (R^2) are shown among plots of each lineage composition; shading around regression lines indicates the 95% CI, and dashed lines indicate slopes do not significantly differ from zero ($p \geq 0.05$). Slopes do not significantly differ with lineage composition ($\chi^2 \leq 2.96$, df = 2, $p > 0.11$). Note the *y*-axis of (a–f) are $\log_{10}$ transformed. Inset pie charts show the independent proportion of variation explained by each predictor (LAI and lineage composition) in an additive model.

tolerance (Canham et al., 1994; Reich et al., 2003; Valladares & Niinemets, 2008). Despite their young age (ca. 10 years old) and potential differences among species in basal area, we found consistent trends among monoculture canopies, with canopies of more shade-tolerant species tending to transmit less light. For instance,

TABLE 3 Coefficients and the significance of terms in mixed-effects models examining net biodiversity effects (NBEs) on canopy transmittance in a variety of wavelengths.

Source	UV	Blue	Red	Far red	Near infrared	Shortwave infrared	Red to far red
Intercept	0.016+	0.017*	0.016	0.011	0.001	0.011	−0.006
NBE LAI	−0.018*	−0.013	−0.005	−0.016	−0.026^{+}	−0.014	−0.087*
Gymno	−0.017	−0.016	−0.012	−0.009	−0.001	−0.008	−0.041
Angio-gymno	−0.026**	−0.026*	−0.024^{+}	−0.030*	−0.027^{+}	−0.027^{+}	−0.065
NBE LAI × gymno	0.012	0.008	0.002	0.007	0.011	0.006	0.089^{+}
NBE LAI × angio-gymno	0.006	0.000	−0.008	−0.005	−0.003	−0.007	0.048
R^2_m	0.20	0.16	0.11	0.20	0.26	0.17	0.11
R^2_c	0.20	0.16	0.11	0.22	0.27	0.19	0.14

Note: Site was treated as a random effect. NBE LAI = net biodiversity effect on leaf area index, gymno = assemblages of gymnosperm species, angio-gymno = assemblages of angiosperm and gymnosperm species (the intercept represents assemblages of angiosperm species).

Abbreviations: LAI, leaf area index; R^2_c, conditional coefficient of determination for fixed and random effects; R^2_m, marginal coefficient of determination for fixed effects.

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{+}p < 0.1$.

canopies of shade-intolerant angiosperm species such as *Betula* spp. tended to transmit more light and, among the gymnosperm species, canopies of shade-tolerant *Picea* spp. transmitted the least light (Figure 2a–f). Relationships between shade tolerance and total transmittance were especially evident among gymnosperms (Pearson's correlation within sites of −0.68 to −0.79), but less so among angiosperms (−0.50 and −0.54 at IDENT-Cloquet and Freiburg, which have almost identical species pools, but 0.38 at FAB-1). Overall, these canopy transmittance patterns of young stands appear to already signal expected shifts toward more shade-tolerant species as forests develop (Messier et al., 1999).

The ratio of red to far-red light transmitted through canopies declined in concert with a decline in the transmittance of PAR, but this relationship systematically differed with the lineage composition of canopies (Figure 3). Such differences in the light quality below canopies composed of needle-leaved gymnosperm and broad-leaved angiosperm species have been shown previously (Federer & Tanner, 1966; Hovi & Rautiainen, 2020; Leuchner et al., 2007; Lieffers et al., 1999; Messier & Bellefleur, 1988; Ross et al., 1986). Our results confirm and extend these findings, showing that the spectral properties of light reaching the understory are influenced by a larger set of canopy species over a broad spectral range from the visible to the short-wave infrared—and that mixed-lineage canopies tend to display intermediate spectral properties.

We found the total amount of foliage within a canopy (i.e., LAI) to be the principal determinant of transmittance of light through canopies, including across wavelengths that plants use as neighborhood context cues to inform patterns of development, growth, and allocation (see Figure 1). Communities of differing composition are known to create canopies with differing LAI (Williams et al., 2021). LAI varied substantially among our tree communities and explained around half (46%–53%) of the variation in canopy transmittance at each of our focal wavelengths, but considerably less variation (16%) in red to far-red transmittance (Figure 4). Canopy transmittance in the red to far-red may thus be influenced more by community differences in leaf optical properties and foliage arrangement.

For a given LAI, we found a significant influence of lineage composition on canopy transmittance in biologically important wavelengths, including in the ratio of red to far-red. The slope of the decline in canopy transmittance with increasing LAI was steeper in angiosperm canopies than in mixed angiosperm-gymnosperm canopies and gymnosperm canopies. While differences in transmittance between angiosperm and gymnosperm communities have been shown previously (Hovi & Rautiainen, 2020; Leuchner et al., 2007; Lieffers et al., 1999; Ross et al., 1986), here we found that mixed species communities result in intermediate transmittance properties, and that these lineage effects emerged primarily due to differences between angiosperms and gymnosperms in within-shoot clumping. Specifically, prior to accounting for within-shoot clumping in LAI ($\mathrm{LAI}_{\mathrm{effective}}$), we did not find significant lineage differences between angiosperms and gymnosperms at any of our focal wavelengths in the relationship between canopy transmittance and $\mathrm{LAI}_{\mathrm{effective}}$ ($\chi^2 \leq 3.24$, df = 2, $p \geq 0.080$)—or the ratio of red to far-red transmittance ($\chi^2 = 1.71$, df = 2, $p = 0.301$; Appendix S1: Figure S4). Our interpretations are based on the assumption that we have obtained reasonable estimates of LAI. We note, however, that the LAI-2000 instrument underestimates LAI of needle-leaved gymnosperm species due to within-shoot clumping (Chen et al., 2006; Gower & Norman, 1991; Majasalmi et al., 2013; Smolander et al., 1994; Sonnentag et al., 2007; Stenberg, 1996), which we accounted for by applying species-specific correction factors from previous studies. Within-shoot clumping is also likely to vary within species, and we do not have data to quantify such variation nor to validate these correction factors at our sites. Moreover, assigning LAI to species in mixed-species canopies is uncertain (Appendix S1: Figure S3). Finally, we ignored the contribution of branches and stems to light interception; their inclusion can have a major impact on estimated carbon flux (Butler et al., 2020). Equations used to predict LAI using the LAI-2000 do not consider differences among stands within or among species in branch and stem light interception, and their exclusion herein likely adds a modest, but real, error to our attempts to link canopy transmittance with LAI.

In theory, the optical properties of individual leaves have the potential to modulate canopy transmittance. While differences in individual leaf transmittance among species and communities were minor relative to differences in canopy transmittance in the UV, blue, and red wavelengths, at longer wavelengths, species differences in leaf-level transmittance were potentially large enough to contribute to the variation among communities in canopy transmittance (Appendix S1: Figure S5). We found differences among communities in leaf transmittance alone had little relationship with observed differences in canopy transmittance (Appendix S1: Table S3), consistent with previous work across angiosperm communities (Messier & Bellefleur, 1988). The impact of the low transmittance of gymnosperm needles through the NIR on canopy transmittance, and thus on the red-to-far-red ratio, is likely compounded by within-shoot clumping. We likely underestimated the influence of leaf optical properties on canopy transmittance because we did not assess the influence of leaf diffuse and specular reflectance, which contribute to potential downward scattering of light (Hovi & Rautiainen, 2020; Knyazikhin et al., 2013). Moreover, simulations with radiative transfer models suggest that increasing the variation among individual leaves in their optical properties may subtly but consistently decrease canopy transmittance, especially in spectral regions beyond PAR (Plekhanova et al., 2021), which warrants further investigation. Reflectance from other surfaces, such as soil, may also shape the spectral profile of light beneath and within canopies.

Variation among communities in the spectral profile of canopy transmittance is likely to arise from both differences in leaf optical properties as well as the arrangement of leaves and architecture of crowns. For PAR transmittance, a dominant role of canopy structure over leaf optical properties has been shown using radiative transfer modeling (Kükenbrink et al., 2021; Plekhanova et al., 2021). Light transmitted directly through canopy gaps—compared with light transmitted through or reflected off leaves—is relatively enriched in red to far-red light. Leaf angle (Yang et al., 2023) and the degree of clumping influence canopy gaps as well as scattering (Hovi & Rautiainen, 2020); for instance, the greater clumping of needle-leaved gymnosperms may contribute to the greater red to far-red transmittance relative to PAR transmittance and to LAI that we observed in gymnosperm canopies (Figures 3 and 4g). In sum, canopy structure strongly influences the UV and PAR, while the interaction of leaf optical properties with canopy structure through scattering disproportionately influences longer wavelengths and thus also red-to-far-red ratios.

Diversity Effects on Canopy Transmittance Were Only Partly Explained by Diversity Effects on LAI

Controlling for species composition by comparing monocultures and mixtures, we also showed that tree diversity affects both the quantity and quality of light transmitted through forest canopies. At least 74% of the observed variation in diversity effects on transmittance in each focal wavelength was neither explained by diversity effects on LAI nor by the lineage composition of canopies (Table 3; Figures 5 and 6). These results suggest that diversity effects on canopy transmittance were likely largely shaped by effects of diversity on the arrangement of foliage or on their leaf optical properties. Mixing species is known to alter the allometry of individual trees (Forrester et al., 2017). Moreover, both interspecific differences and neighborhood-induced intraspecific differences in crown shapes influence how they fit together in space (spatial crown complementarity; Williams et al., 2017), tending to result in increased canopy packing in mixtures (Jucker et al., 2015; Pretzsch, 2014). Species mixtures where crowns are more complementary and more completely fill canopy space may have less direct light transmittance—consistent with the observed tendency of lower red to far-red transmittance in mixtures (Figure 6g). Leaf optical properties may also differ in mixtures as a consequence of plasticity (Czyż et al., 2023; Li et al., 2023), given that species may express different leaf trait values in different communities (e.g., Benavides et al., 2019; Felix et al., 2023; Williams et al., 2020).

Functional Implications and Next Steps

Ultimately, we are interested in understanding the biological and ecological implications of differences among communities in canopy transmittance, including the extent to which community composition and diversity shape light quality cues that influence tree architecture as well as the production of chemical compounds. It is known that the spectral composition of light can mediate shifts in plant function that shape their survival, growth, and allocation to defense compounds (Ballaré & Pierik, 2017; Garcia-Molina et al., 2020; Pierik & Ballaré, 2021; Smith, 1982). For example, chemical compounds known to be involved in light exposure responses vary through individual tree crowns (Valdés-Correcher et al., 2020; Volf et al., 2022). However, whether and how variation in canopy light transmittance affects the production of these defense compounds remains to be demonstrated. If lower ratios of red to far-red light mean growth is prioritized over defense, lower ratios of red to far-red transmittance in species mixtures (Figure 6g) might lead to enhanced growth at the cost of greater susceptibility to herbivory or oxidative stress, with potential consequences for both the productivity and resilience of forests.

In this study, we focused on canopy transmittance at a single point in time mid-season during peak leaf biomass across a diverse set of developing tree communities in three different tree diversity experiments. Yet, the spectral profiles of canopy transmittance may vary spatially and temporally in complex ways: The intensity of incoming irradiance varies markedly from seconds to seasons to years (Pearcy, 1990), the spectral quality of transmitted light varies with sun angle and atmospheric conditions (Lieffers et al., 1999; Leuchner et al., 2007; Hertel et al., 2011), and light quality will change through time as forests develop. Given these sources of variability, understanding the biological significance of light quality cues within complex canopies is challenging. Nevertheless, we saw that the transmittance of light at wavelengths plants are known to sense differed among diverse tree canopies—and, controlling for species composition, we observed that tree diversity itself affected the spectral properties of canopy transmittance. Moreover, composition and diversity affected canopy transmittance in largely predictable ways, via effects on LAI as well as leaf transmittance and canopy structure. Coupled with knowledge of how light quality cues can shape plant function (e.g., Pierik & Ballaré, 2021), our findings set the scene for differences in spectral light cues through forest canopies—as mediated by the composition and diversity of tree communities—to shape trait expression and the allocation and growth of trees and of understory plants. These light quality cues may serve as a biological mechanism by which tree composition and diversity affect forest ecosystem function, including their productivity and susceptibility to herbivory or disease.

AUTHOR CONTRIBUTIONS

This highly collaborative study from members of ASCEND was initially conceptualized by Meredith C. Schuman, Kyle R. Kovach, and Laura J. Williams. The tree diversity experiments were designed and implemented by Christian Messier, Peter B. Reich, Jeannine Cavender-Bares, Michael Scherer-Lorenzen, Alain Paquette, and Artur Stefanski. Field work at IDENT-Freiburg was led by Jeannine Cavender-Bares and Meredith C. Schuman with assistance from Johanna Klama, Aboubakr Moradi, Peter Hajek, and Michael Scherer-Lorenzen. Field work at IDENT-Cloquet and FAB-1 was led by Kyle R. Kovach, Artur Stefanski, Maria H. Park, Raimundo Bermudez, and Laura J. Williams with assistance from Catherine Glenn-Stone and Ethan E. Butler. Spectral data were processed by J. Antonio Guzmán Q., Kyle R. Kovach, and Laura J. Williams. Laura J. Williams analyzed the data and wrote the original draft. All authors contributed substantially to conceptual development and revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Williams et al., 2024) are available in DRUM (the Data Repository for University of Minnesota) at https://doi.org/10.13020/z64a-da16.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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