Tansley review

Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications

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Summary

Rising temperatures are influencing forests on many scales, with potentially strong variation vertically across forest strata. Using published research and new analyses, we evaluate how microclimate and leaf temperatures, traits, and gas exchange vary vertically in forests, shaping tree, and ecosystem ecology. In closed-canopy forests, upper canopy leaves are exposed to the highest solar radiation and evaporative demand, which can elevate leaf temperature (Tleaf), particularly when transpirational cooling is curtailed by limited stomatal conductance. However, foliar traits also vary across height or light gradients, partially mitigating and protecting against the elevation of upper canopy Tleaf. Leaf metabolism generally increases with height across the vertical gradient, yet differences in thermal sensitivity across the gradient appear modest. Scaling from leaves to trees, canopy trees have higher absolute metabolic capacity and growth, yet are more vulnerable to drought and damaging Tleaf than their smaller counterparts, particularly under climate change. By contrast, understory trees experience fewer extreme high Tleaf’s but have fewer cooling mechanisms and thus may be strongly impacted by warming under some conditions, particularly when exposed to a harsher microenvironment through canopy disturbance. As the climate changes, integrating the patterns and mechanisms reviewed here into models will be critical to forecasting forest–climate feedback.
I. Introduction

Global average temperatures have risen 1.2°C since 1900 (Rohde & Hausfather, 2020) and are expected to reach +1.5°C by 2040 (IPCC, 2021), accompanied by increasing severity and frequency of heat waves and hotter droughts (Meehl & Tebaldi, 2004; IPCC, 2021). These changes are affecting tree metabolism and forest ecosystem function (Breshears et al., 2021; Pörtner et al., 2021) by altering rates of photosynthesis and respiration (Breshears et al., 2021; Scafaro et al., 2021), causing foliar damage during heat waves (Corlett, 2011; O’Sullivan et al., 2017), and reducing growth and elevating mortality during drought (McDowell et al., 2020; Breshears et al., 2021). The resulting feedback to climate and carbon storage, and changes in albedo and hydrology will in turn impact the future trajectory of climate change (Bonan, 2016), yet future forest dynamics remain one of the largest sources of uncertainty in Earth system model climate change projections (Friedlingstein et al., 2006; Krause et al., 2018; Arora et al., 2020).

Future forest dynamics will depend on how climate change impacts trees of varying height and crown position. Forests are vertically stratified, and canopies moderate climatic conditions (Ozanne, 2003; Nakamura et al., 2017), including buffering understory microclimates from extreme meteorological conditions (Zellweger et al., 2019). Vertical gradients in biophysical variables such as temperature, light, wind, humidity, and carbon dioxide (CO₂) concentrations influence leaf temperatures, traits, and metabolism, with implications for whole-plant performance (Michaletz et al., 2016; Fauset et al., 2018). Although forest vertical stratification strongly influences plant metabolism, demography, and ecology, we lack comprehensive understanding of these gradients (but see Niinemets & Valladares, 2004). Importantly, this limits our ability to understand how warming temperatures will affect leaf-level metabolism, whole-plant performance, and, in turn, forest dynamics, biodiversity, energy balance, ecosystem function, and biosphere–atmosphere interactions.

Here, we review vertical gradients in the biophysical environment and plant form and function in forests, focusing on five themes (Fig. 1): the biophysical environment; leaf temperature (T_leaf); the leaf traits that most strongly influence T_leaf and thermal tolerance; leaf gas exchange and its thermal sensitivity; and, tree and ecosystem ecology. We then consider the implications for understanding forest responses to global change and how they scale across space and time.

II. Review of vertical gradients

1. The biophysical environment

The biophysical environment, defined here to include the physical structure of the vegetation and associated micrometeorological conditions, varies vertically from the forest floor to the top of the canopy (Figs 1, 2), with micrometeorological conditions largely determined by forest structure. In this section, we review the existing literature and analyze data on vegetation structure and vertical microclimate profiles from forested sites within the US National Ecological Observatory Network (NEON; Fig. 2; Supporting Information S1; Methods S1). Although we focus on vertical gradients, it is important to note that in heterogeneous canopies with high gap fractions and large variation in tree height, or at forest edges, the biophysical environment can be more closely linked to the distance from the outer edge of vegetation than to height (Lowman & Rinker, 1995).

Foliage

Canopy foliage is the primary physical barrier between the atmosphere and the forest floor, buffering multiple aspects of the understory conditions from large fluctuations in conditions experienced above the canopy. It strongly influences – and is influenced by – the vertical biophysical gradient. Vertical patterns in leaf area density (i.e. leaf area per unit volume) differ across forests (Figs 2a,b, S1). In tropical and temperate forests with dense broadleaf canopies, leaf area density is generally highest in the canopy layer (i.e. that formed by the crowns of dominant trees), but understory leaf area density is often high as well, sometimes causing undulating patterns with height (Parker et al., 1989; Ashton & Hall, 1992; Koike & Syahbuddin, 1993; Domingues et al., 2005). In forests with more open upper canopies, including many needleleaf forests, leaf area density can be greatest in the lower canopy or understory (Baldocchi et al., 1997; Law et al., 2001; Bonan, 2016; Hanberry et al., 2020). Soil moisture conditions, topography, and gap formations following disturbances all alter foliage patterns (Stark et al., 2012; de Almeida et al., 2016; Bonan, 2016; Hanberry et al., 2020). In addition, seasonally dry and wet conditions, deciduousness, and phenology contribute to temporally shifting leaf area density patterns (Tang & Dubayah, 2017; Parker et al., 2019; Smith et al., 2019; Nunes et al., 2022). In this review, we focus on growing season conditions unless otherwise noted.

Light

The intensity of visible and photosynthetically active radiation (PAR, 400–700 nm) decreases from the canopy top to the forest floor, with a profile whose shape is modified by leaf area density, leaf clumping, canopy height, and vertical structure across species and forest types (Figs 2d, S1; Koike et al., 2001; Béland & Baldocchi, 2021; Bin et al., 2022). Canopy foliage absorbs a large portion of PAR (400–700 nm) and selectively filters light, thereby altering the spectrum of PAR received in the lower canopy and understory layers. The ratio of red (c. 685–690 nm) to far red (c. 730–740 nm) light declines along with total PAR with increasing depth in the canopy, and understories receive diffuse light enriched in near-infrared radiation (700–1000 nm; de Castro, 2000; Poorter et al., 2000). Midcanopies and understories experience a highly dynamic light environment due to sunflecks, or brief increases in direct solar radiation, caused by small canopy gaps, wind-induced canopy movements, or the sun’s passage across a dynamically structured canopy surface (Way & Peary, 2012). This light gradient is more pronounced in dense canopies, including broadleaf and mixed forests, than in forests with more open upper canopies, including many conifer forests (Figs 2d, S1; Chazdon & Fetcher, 1984; Baldocchi et al., 1997; Bartemucci et al., 2006; Tyms et al., 2017; Parker et al., 2019). This light gradient drives variation in leaf temperature (Section II.2), traits (Section II.3), and photosynthesis (see Section II.4, subsection ‘Photosynthesis’).
Turbulent transport and wind

Vertical transport in forest canopies is dominated by turbulent transport, making vertical profiles of wind speed, water vapor, CO2, and temperature more difficult to predict and to generalize on the basis of theoretical first principles than radiation profiles. Above the canopy, turbulent transport typically mimics diffusion—that is, vertical fluxes of heat, mass, and momentum are proportional to their respective vertical gradients, and to transfer coefficients (eddy diffusivities; Penman & Long, 1960)—such that wind speed declines logarithmically with proximity to the canopy surface (Monteith & Unsworth, 2013). Interaction with a plant canopy also attenuates wind, causing wind speed to decline through the canopy, for example, small plant elements can rapidly dissipate momentum within dense canopies (Raupach & Shaw, 1982; Baldocchi & Meyers, 1988). Within canopies, however, transport often fails to mimic diffusion—for example, transport of momentum (Shaw, 1977) or heat (Raupach, 1987) may occur in the direction opposite to that predicted by gradients of wind speed or temperature, respectively—making vertical wind profiles difficult to generalize from first principles (Denmead & Bradley, 1987; Meyers & Paw, 1987; Raupach, 1989; Katul & Albertson, 1999; Harman & Finnigan, 2007). Such counter-gradient transport may arise from the intermittent generation, at the canopy surface, of large wakes or coherent eddy structures that periodically dip down through the canopy, gathering packets of warmed, humidified, and CO2-enriched or depleted air from beneath and within the canopy and flushing them to the atmosphere above (Finnigan, 1979; Baldocchi & Meyers, 1991). These ‘sweep-eject’ events can couple understory conditions more directly to conditions above the canopy than beneath.

Despite these complexities of within-canopy transport, wind speeds are generally much higher at the top of the canopy than...
Fig. 2 Vertical gradients in the biophysical environment for six USA forest sites in the National Ecological Observatory Network (NEON). Height profiles, normalized relative to the top of the canopy, are shown for: growing season (a) modeled leaf area density, (b) estimated proportion of sun leaves, and (c) proportion of light incident to the top of the canopy (as fraction relative to top of canopy), and for July mean ± 1 SD for (d) maximum photosynthetically active radiation (PAR), (e) maximum wind speed, (f) minimum humidity (min RH), (g) maximum air temperature (T\textsubscript{air}), and (h) maximum biological temperature (T\textsubscript{bio}). Measurements extend from ground level (normalized height = 0 m) to the top of the canopy (horizontal dashed line at normalized height = 1) or above (d–g). Variables shown in (a–c) are derived from LiDAR, and those shown in (d–h) from micrometeorological tower data. Sites, which represent a variety of forest structures, include a mixed northern hardwood forest (Harvard Forest, MA; HARV), a subtropical longleaf pine savanna (Ordway-Swisher Biological Station, FL; OSBS), a tropical montane broadleaf evergreen forest (Pu‘u Maka‘ala Natural Area Reserve, Hawai‘i; PUUM), two temperate broadleaf forests (Smithsonian Conservation Biology Institute, VA, SCBI; Smithsonian Environmental Research Center, MD, SERC), and a coniferous forest (Wind River Experimental Forests, WA; WREF). Further site information is given in Supporting Information Table S1 and analysis details in Methods S1. Vertical profiles in micrometeorological variables (d–h) at all forested NEON sites are shown in Fig. S1.

within or beneath (Jiao-jun et al., 2004; Jucker et al., 2018). This holds true across the range of forest types (Figs 2e, S1; Barnard & Bauerle, 2016; Hanberry et al., 2018, 2020; Jucker et al., 2018; Muller et al., 2021) and savannas (Curtis et al., 2019; Johnston et al., 2022). As a result, upper canopy leaves have substantially higher boundary layer conductance (g\textsubscript{d}) and therefore greater potential for exchange of both mass and sensible heat exchange (Sections II.2 and the II.4 subsection ‘Conductance’).

Atmospheric concentrations of CO\textsubscript{2} and water vapor Atmospheric CO\textsubscript{2} concentrations tend to be higher near the ground at night, associated with plant and soil respiration, but the elevated CO\textsubscript{2} quickly dissipates during the day such that CO\textsubscript{2} concentration differences are negligible for most of the day when photosynthesis is occurring (Brooks et al., 1997; Yang et al., 1999; Koike et al., 2001). While understory seedlings may benefit modestly from higher CO\textsubscript{2} concentrations near the ground during some parts of the day (e.g., 6% of C fixation from recently respired CO\textsubscript{2}; Brooks et al., 1997), gradients in CO\textsubscript{2} concentrations likely have little effect on energy balance and metabolism of trees across the vertical gradient (Brooks et al., 1997).

Relative humidity (RH) tends to be higher in the understory and decreases with height, although this trend is absent in open forests (Figs 2f, S1; Jucker et al., 2018; Bin et al., 2022). Dense-canopy forests maintain higher daily maximum RH in the understory than open forests and nearby open areas, an effect that is greater in wetter conditions, and warmer months (von Arx et al., 2012; Hanberry et al., 2020). In combination with air temperature (T\textsubscript{air}) and T\textsubscript{leaf}, RH determines leaf-to-air vapor pressure deficit (VPD) – the driving force of water loss from leaves – which tends to be greater in the upper canopy and canopy gaps than in the understory (Niinemets & Valladares, 2004; Tymen et al., 2017; Faust et al., 2018). Especially when canopy height and leaf area index (LAI) are large, maximum T\textsubscript{air} and VPD are reduced in the understory (Jucker et al., 2018).
implication is that upper canopy leaves have higher $g_s$ and associated potential for water and heat loss than understory leaves (Sections II.2 and the II.4 subsection ‘Conductance’).

Air temperature Vertical gradients in air temperature ($T_{air}$) vary widely (Figs 2, S1), depending on factors such as vegetation type, local topography, vertical air mixing, cloud cover, sensible heat emissions, and times of day and year (Zellweger et al., 2019; De Frenne et al., 2021). Commonly, attenuation of radiation and vertical transport of sensible heat by the canopy buffers the lower canopy and understory from large diel and seasonal swings in air temperature (Zellweger et al., 2019; De Frenne et al., 2021; Haesen et al., 2021). Diel temperature range is typically smaller beneath dense canopies than above, resulting from lower maximum daytime $T_{air}$ and warmer nighttime minimum $T_{air}$ than beneath open canopies or in nearby clearings (von Arx et al., 2012; Zellweger et al., 2019; De Frenne et al., 2021). Notably, buffering against high maximum daytime $T_{air}$ becomes weaker and can be reversed as canopies become more open (Fig. S1; Curtis et al., 2019; Meussen et al., 2021). Analogous to a ‘canopy greenhouse effect’, in open forests, below-canopy maximum $T_{air}$ can be warmer than canopy $T_{air}$ due to turbulent air mixing and interception of thermal radiative flux from the soil and the canopy by lower canopy layers (e.g. OSBS, Figs 2g, S1b; Banerjee et al., 2017; Curtis et al., 2019; Muller et al., 2021). These usually modest gradients in $T_{air}$ combine with the above-described gradients in micrometeorological conditions to shape $T_{leaf}$ patterns within canopies.

2. Leaf temperature

$T_{leaf}$ is strongly tied to, and usually within a few degrees of, $T_{air}$ (Rey-Sánchez et al., 2016; Drake et al., 2020) but can be substantially warmer or cooler under certain conditions (Notes S1; Doughty & Goulden, 2008; Vogel, 2009; Rey-Sánchez et al., 2016). Deviation of $T_{leaf}$ from $T_{air}$ is influenced by other micrometeorological drivers and by leaf traits and stomatal conductance ($g_s$; Fig. 3; Notes S1), all of which vary across forest vertical gradients (Fig. 1). High radiation in the upper canopy implies that upper canopy leaves often have higher $T_{leaf} - T_{air}$ and thus are often warmer than understory leaves (Fig. 3a). However, higher wind speeds reduce $T_{leaf} - T_{air}$ (Fig. 3b; Niinemets & Valladares, 2004; Bonan, 2016). In addition, adaptive leaf traits that increase $g_s$ and $g_m$, such as small size and high stomatal density (Notes S1; Sections II.3 and II.4 subsection ‘Conductance’), mediate the direct effects of solar radiation on upper canopy leaves and result in higher rates of heat loss (Fig. 3b–e). By contrast, in the lower canopy, greater RH (reduced VPD) and lower wind speeds (reduced $g_m$) may limit leaf cooling via latent heat flux, increasing $T_{leaf}$ (Tibbitts, 1979; Perez & Feeley, 2018). Leaves in these normally shaded locations can experience rapid light and temperature surges during sunflecks (> 10°C; Way & Pearcy, 2012).

Elevation of $T_{leaf}$ above $T_{air}$ varies with micrometeorological conditions. During drought (associated with conditions that are hot and dry, with higher-than-average solar radiation), when $g_s$ is limiting, $T_{leaf} - T_{air}$ will tend to be higher in the upper canopy than in the understory (Fig. 3). This is because sun leaves are exposed to higher irradiance and VPD and therefore have stronger $g_s$ limitation than shade leaves (Fig. 3e; Leigh et al., 2017; Fauset et al., 2018). By contrast, under conditions conducive to stomatal opening, higher wind speeds and $g_s$ enable cooling in the upper canopy, whereas lower wind and $g_s$ in the understory limit evaporative cooling (Fig. 3b,d; Roberts et al., 1990; Martin et al., 1999; Leigh et al., 2017). Thus, while understory and within-canopy shade leaves can remain cooler under lower radiation, their environment is less conducive to dissipating excess heat compared with upper canopy leaves, because wind speeds and hence $g_s$ are generally smaller in the lower canopy (Roberts et al., 1990; Martin et al., 1999). Limitations in heat dissipation in shade leaves, together with physiological propensities, may cause above-optimal $T_{leaf}$ under slight heat or drought stress or during sunflecks (Schymanski et al., 2013; Leigh et al., 2017; Song et al., 2020). In addition to lower wind speeds, higher RH (lower VPD) in the understory and inner canopy also reduces evaporative cooling (because evaporation rate generally increases with VPD), thus increasing $T_{leaf} - T_{air}$ (Fig. 3c; Tibbitts, 1979; Dietz et al., 2007; Perez & Feeley, 2018; Song et al., 2020; Konrad et al., 2021).

Vertical $T_{leaf}$ gradients also vary with canopy structure (Figs 2h, S1). Forests with closed canopies and high LAI, including tropical and temperate broadleaf forests, act as a parasol, absorbing most incoming radiation and preventing vertical air mixing in the understory. Therefore, in these forests, leaves in the upper canopy can experience greater $T_{leaf} - T_{air}$ and higher maximum $T_{leaf}$ than lower canopy leaves, in some cases exceeding photosynthetic temperature optima ($T_{opt}$) because of $g_s$ limitation and high radiation (Doughty & Goulden, 2008; Mau et al., 2018; Carter et al., 2021; Miller et al., 2021). By contrast, open canopies with lower LAI allow more vertical air mixing and sunlight into the understory, which can either neutralize a $T_{leaf}$ gradient or elevate $T_{leaf} - T_{air}$ at lower heights relative to the upper canopy (Martin et al., 1999; Zweifel et al., 2002; Muller et al., 2021). The latter can result from a combination of still air at lower heights, sunflecks or the ‘canopy greenhouse effect’ (see Section II.1 subsection ‘Air temperature’), and the tendency for shade leaves to have lower $g_s$ (Section II.3; Schymanski et al., 2013; Hardwick et al., 2015).

Similarly, in very open forests or savannas, trees growing close to the ground can experience greater heat stress in their lower-than-upper canopies due to the heat from the soil increasing $T_{leaf}$ near the ground (Hadley & Smith, 1987; Curtis et al., 2019; Johnston et al., 2022). One of the few studies combining drone LiDAR and thermal data found strong vertical gradients in midday plant temperature with c. 5°C cooler temperatures lower in the vertical profile of a dense subalpine stand in the alpine Eastern Swiss Alps (Webster et al., 2018). However, the opposite trend was observed for a lone tree surrounded by grass in a California open oak woodland, with cooler temperatures at the top of the crown, indicating a strong influence of closed-canopy shading on vertical temperature gradients (Johnston et al., 2022).

3. Leaf traits

Anatomical, structural, and biochemical leaf traits vary vertically across forest strata (Table 1; Sack et al., 2006; Niinemets
Fig. 3 Theoretical expectations for variation in the difference between leaf and air temperatures, $T_{\text{leaf}} - T_{\text{air}}$, in response to (a) shortwave radiation, (b) wind speed, (c) relative humidity (RH), (d) leaf characteristic dimension, and (e) stomatal conductance. Leaf temperatures were modeled using the tealeaves R package of Muir (2019) parameterized to represent a broadleaf species (Quercus rubra) in a mesic temperate forest (Harvard Forest, MA, USA) under hypothetical moist and drought conditions, as detailed in Supporting Information Methods S2. In each scenario, the independent variable was allowed to vary while other parameters were held constant at the values given in the table of biophysical constants. Dots along each line correspond to the biophysical constant assigned for the independent variable in the other scenarios, and therefore represent the modeled value for $T_{\text{leaf}} - T_{\text{air}}$ with all parameters set to the biophysical constants given in the table. Biophysical constants in the table include the following: shortwave radiation (swr), wind speed (ws), relative humidity (RH), leaf characteristic dimension (lcd), stomatal conductance ($g_s$, mol m$^{-2}$ s$^{-1}$), and air temperature ($T_{\text{air}}$).

et al., 2015a; Chen et al., 2020), shaping vertical profiles of leaf temperature, gas exchange, and thermal sensitivity (Zwieniecki et al., 2004; Michaletz et al., 2015, 2016). Vertical variation in leaf structure and composition has long been recognized, with sun and shade leaf traits distinguished for over a century (Haberlandt, 1914; Salisbury, 1928). Early work attributed differences among leaves to sun vs shade (Wylie, 1951; Vogel, 1968), and this tendency grew given the parallel differences observed for plants grown in sun vs shade (Boardman, 1977; Abrams & Kubiske, 1990). More recent work has extended the focus from light alone to height in the vertical profile, as the latter shapes differences in leaf structure and function that can partially mitigate the effects of gravity and hydraulic pathlength on leaves higher up in the canopy (Koch et al., 2004; Burgess et al., 2006; Sack et al., 2006). For example, leaf mass per area (LMA), photosynthetic capacity ($A_{\text{max}}$ per area), and $g_s$ have been observed to increase with height, independently of light (Cavender-Bares & Bazzaz, 2000; Thomas & Winner, 2002; Houter & Pons, 2012; Bin et al., 2022). Thus, leaves develop differently according to the irradiance and hydraulic stress associated with their canopy location, height, and evaporative load, with additional potential influences of branch ontogenetic stage (Sack et al., 2006; Niinemets, 2010; de Casas et al., 2011; Niinemets et al., 2015b; Keenan & Niinemets, 2016; Chen et al., 2020; Carter et al., 2021; Bin et al., 2022). Plasticity throughout the canopy may emerge when development of new leaves is influenced by information from adjacent mature leaves or apical meristems and may also acclimate during and after expansion to the current microclimate (Zwieniecki et al., 2004). Overall, leaf biochemistry, anatomy, and structure may be optimized to local conditions (Niinemets, 2007; Lloyd et al., 2010; Hikosaka, 2014; Kitao et al., 2012; Buckley, 2021). However, we lack a cohesive framework for integrating the many differences in leaf traits throughout the canopy. Rather, much of our understanding of trait coordination is based on the leaf economics spectrum concept developed across diverse species using sun leaves (Wright et al., 2004; Keenan & Niinemets, 2016; Chen et al., 2020). As canopy shade is known to alter these trait relationships (Osnas et al., 2018), further research is needed to characterize trait relationships and responses vertically through the full range of canopy microenvironments.

Across the vertical gradient, traits vary: (1) within individuals, across height and light gradients (Zwieniecki et al., 2004; Sack et al., 2006; Bin et al., 2022); (2) across individuals of the same species, often representing an ontogenetic trajectory from the
understory to the canopy (Niinemets, 2010; Carter et al., 2021); and, (3) among understory and canopy species (Lloyd et al., 2010). Most studies characterizing variation in leaf traits or metabolism examine intraspecific patterns (Categories 1 and 2), which are therefore the main focus of this review (Table 1). Generally, the pattern of fundamental trait adaptations to light gradients across forest species is similar to within-species trends (Thomas & Winner, 2002; Rozendaal et al., 2006; Cavalieri et al., 2010; Lloyd et al., 2010; Houter & Pons, 2012; Bin et al., 2022); however, vertical trends vary across trees (Lloyd et al., 2010), and countergradient variation can exist (Lusk et al., 2008). Many leaf physiological parameters can be estimated based on foliage height profiles (Cavaleri et al., 2010; Lloyd et al., 2010).

**Leaf anatomy and morphology** Sun leaves have anatomical, morphological, and physiological traits that reduce $T_{\text{leaf}}$ through higher conductance ($g_s$ or maximal $g_s$) and/or reflectance (Table 1). Thus, sun leaves are generally smaller and thicker, with higher LMA, and are more deeply lobed (Fig. 3; Vogel, 1968; Zwieniecki et al., 2004; Sack et al., 2006; Leight et al., 2017), but with greater leaf packing and clumping (which reduces $g_s$). Steeper leaf angles reduce midday radiation loads and thereby decreasing $T_{\text{leaf}} - T_{\text{air}}$ (Ball et al., 1988; Niinemets, 1998), while higher trichome density increases reflectance, also decreasing radiation load. Furthermore, sun leaves tend to have higher stomatal and vein densities, which facilitate evaporative cooling by enabling higher $g_s$ (see Section II.4 subsection ‘Conductance’; Zwieniecki et al., 2004). Yet, sun leaves also have adaptations to limit water stress, particularly in drier climates, including greater cuticle thickness and higher trichome density (which may reduce or increase $g_s$; Schreuder et al., 2001; Ichie et al., 2016). By contrast, shade leaves have traits that maximize light capture (e.g. lower LMA and greater light absorptance per unit biomass), but larger leaves and lower transpiration make them more prone to overheating than sun leaves (de Casas et al., 2011; Schymanski et al., 2013; Leight et al., 2017). In open canopies, where light is comparatively homogeneous, leaf traits may be shaped more by maximum $T_{\text{air}}$ and VPD stress than by light (Mediavilla et al., 2019).

**Leaf optical properties** Leaf optical properties are influenced by anatomical, morphological, and biochemical traits that vary throughout the canopy (see Section II.3 subsections ‘Leaf anatomy and morphology’ and ‘Metabolic capacity and efficiency’). High in the canopy, high light absorptance can lead to photoinhibition and would, in part, be mitigated by the canopy, high light absorptance can lead to photoinhibition and morphology’ and ‘Metabolic capacity and efficiency’). High in contrast, shade leaves have lower LMA and absorb more light per unit mass investment, as well as denser chloroplast layers and a greater proportion of spongy mesophyll, more effective for capturing diffuse light (Table 1; Lee et al., 1990; Poorter et al., 1995, 2000).

**Metabolic capacity and efficiency** Most leaf biochemical traits also vary across light and height gradients (Table 1), both shaping and resulting from gradients in metabolism (Section II.4). Sun leaves have higher area-based concentrations of elements such as nitrogen ($N_{\text{area}}$) and phosphorus ($P_{\text{area}}$) that are critical for respiration (Meir et al., 2001; Weerasinghe et al., 2014) and photosynthesis (Niinemets & Valladares, 2004; Weerasinghe et al., 2014; Scartazza et al., 2016). Increases in chlorophyll $a/b$ ratios with height reflect greater light availability in the upper canopy, while greater chlorophyll concentrations at lower heights increase PAR absorptance efficiency of shade leaves (Table 1). Higher photosynthetic rates (area based) and more frequent stomatal closure in sun-exposed canopies (Section II.4) reduce intercellular CO$_2$ concentrations and increase leaf δ$^{13}$C (Table 1).

**Biochemical protection against foliage light and heat damage** Biochemical protection against light and heat damage increases with peak radiation loads and thus tends to be higher in the upper canopy, which is subject to higher $T_{\text{leaf}}$ and hydraulic limitations, than in the understory (Table 1). More frequent stomatal closure in upper canopy leaves (Section II.4) reduces their capacity to use light energy for photochemistry, thereby requiring a high capacity to dissipate excess light energy and protect against photoinhibition (Niinemets, 2007). Accumulation of excess light energy causes overreduction of the electron transport chain and the formation of harmful reactive oxygen species (Niyogi, 2000; Suzuki & Mittler, 2006). A ubiquitous defense is a rapidly inducible nonphotochemical quenching (NPQ) mechanism that responds to the increased thylakoid pH gradient caused by excess light (Niyogi, 2000; Goss & Lepetit, 2015). This form of NPQ entails interconversion of xanthophyll cycle pigments — violaxanthin, antheraxanthin, and zeaxanthin (VAZ) — which regulates the capacity for de-excitation of chlorophyll through thermal dissipation instead of photochemistry. Leaves in higher light environments show a greater capacity for NPQ and higher concentrations of VAZ as well as other carotenoids (e.g. beta carotene and lutein) employed as antioxidant defenses (Table 1; Niinemets et al., 1998; García-Plazaola et al., 2004; Scartazza et al., 2016). By contrast, to maximize photosynthesis and minimize damage during $T_{\text{leaf}}$ surges caused by sunflecks (Section II.2), shade-acclimated leaves tend to induce photochemical processes more quickly (Urban et al., 2007) and also show a steeper response of NPQ to light than sun-acclimated upper canopy leaves (Scartazza et al., 2016).

Heat-sensitive, light-dependent (photosynthetically linked) emissions of volatile organic compounds (VOCs), including isoprene and monoterpenes, enhance photosynthetic thermal tolerance by regulating antioxidant defenses and other metabolic processes (Copolovici et al., 2005; Sharkey et al., 2008; Vickers et al., 2009; Riedmeier et al., 2017; Taylor et al., 2019; Monson et al., 2021). In contrast to VOCs stored in oils that are released passively by heat and wounding, such as the monoterpenes...
Table 1 Summary of typically observed variation in leaf traits and its thermal sensitivity across the vertical gradient and/or between sun and shade leaves.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Symbol</th>
<th>Units</th>
<th>Response</th>
<th>Forest type(s)</th>
<th>Reference(s)</th>
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<tbody>
<tr>
<td>Leaf anatomy and morphological traits</td>
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<tr>
<td>Leaf area</td>
<td>LA</td>
<td>cm²</td>
<td>↓ H</td>
<td>TrB, TeB, BoN</td>
<td>7, 8, 10</td>
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<tr>
<td>Leaf mass per area (or inverse of specific leaf area)</td>
<td>LMA (or SLA)</td>
<td>g cm⁻²</td>
<td>↑ H</td>
<td>TrB, TeB, BoN, BoN</td>
<td>1, 55, 64, 7, 2, 3, 4, 6</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>µm</td>
<td></td>
<td>↑ H</td>
<td>TrB, TeB, TeN, BoN</td>
<td>1, 7, 2, 3, 5, 6</td>
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<tr>
<td>Leaf density</td>
<td>g cm⁻³</td>
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<td>↑ H</td>
<td>TrB, TeB, TeN</td>
<td>15, 11, 2, 13, 16</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>µm</td>
<td></td>
<td>↑ L</td>
<td>TrB, TeB, TeN</td>
<td>11, 15, 2, 5</td>
</tr>
<tr>
<td>Pinnate lobation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf packing</td>
<td>n cm⁻¹ stem</td>
<td></td>
<td>↑ L</td>
<td>TeN</td>
<td>25, 26</td>
</tr>
<tr>
<td>Blade inclination angle (vertical)</td>
<td>φB</td>
<td>°</td>
<td>↑ H</td>
<td>TrB, TeB</td>
<td>21, 22, 23</td>
</tr>
<tr>
<td>Trichome density</td>
<td>mm⁻²</td>
<td></td>
<td>↑ H</td>
<td>TrB, TeB</td>
<td>21, 24, 22, 48</td>
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<tr>
<td>Stomatal density</td>
<td>Ds</td>
<td>mm⁻²</td>
<td>↑ H</td>
<td>TrB, TeB</td>
<td>17</td>
</tr>
<tr>
<td>Total vein density</td>
<td>VLA</td>
<td>mm mm⁻²</td>
<td>↑ L</td>
<td>TrB, TeB, TeN, BoN</td>
<td>11, 12, 3, 13, 4</td>
</tr>
<tr>
<td>Minor vein density</td>
<td>VLAmin</td>
<td>mm mm⁻²</td>
<td>↑ H</td>
<td>TrB, TeB, TeN</td>
<td>46</td>
</tr>
<tr>
<td>Upper cuticle thickness</td>
<td>CT</td>
<td>µm</td>
<td>↑ L</td>
<td>TrB, TeB, TeN</td>
<td>27, 4</td>
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<tr>
<td>Leaf optical properties</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PAR absorptance</td>
<td>%</td>
<td></td>
<td>↑ L</td>
<td>TrB</td>
<td>42, 45</td>
</tr>
<tr>
<td>Absorptance efficiency per unit biomass</td>
<td>% g⁻¹</td>
<td></td>
<td>↓ H</td>
<td>TrB</td>
<td>42, 45</td>
</tr>
<tr>
<td>PAR transmittance</td>
<td>%</td>
<td></td>
<td>↓ L</td>
<td>TrB</td>
<td>42, 45</td>
</tr>
<tr>
<td>Reflectance</td>
<td>%</td>
<td></td>
<td>≈  H</td>
<td>TrB</td>
<td>42, 45</td>
</tr>
<tr>
<td>Traits related to metabolic capacity and efficiency</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Nitrogen content</td>
<td>N</td>
<td>g m⁻²</td>
<td>↑ H</td>
<td>TrB, TeB, TeN, BoN</td>
<td>55, 64, 7, 29, 30, 32, 31, 9</td>
</tr>
<tr>
<td>Phosphorus content</td>
<td>P</td>
<td>g m⁻²</td>
<td>↑ L</td>
<td>TrB, TeB, TeN</td>
<td>55, 15, 29, 30, 32, 5</td>
</tr>
<tr>
<td>Chlorophyll content</td>
<td>Chl</td>
<td>mg cm⁻²</td>
<td>↓ H</td>
<td>TrB, TeB</td>
<td>40, 41</td>
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<tr>
<td>Chlorophyll a/b ratio</td>
<td>chla/b</td>
<td>mol mol⁻¹</td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>42, 30, 6</td>
</tr>
<tr>
<td>Carbon isotope ratio</td>
<td>δ¹³C</td>
<td>%</td>
<td>↑ L</td>
<td>TrB, TeB, TeN</td>
<td>55, 64, 7, 43, 31</td>
</tr>
<tr>
<td>Intercellular CO₂ concentration</td>
<td>Cᵢ</td>
<td>µmol mol⁻¹</td>
<td>↓ H</td>
<td>TrB, BoN</td>
<td>51, 30, 44</td>
</tr>
<tr>
<td>Biochemical protection against light and heat damage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>β-Carotene and lutein</td>
<td>µmol m⁻²</td>
<td></td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>30, 42, 6</td>
</tr>
<tr>
<td>Xanthophyll cycle pigments</td>
<td>VAZ</td>
<td>µmol m⁻²</td>
<td>↑ H</td>
<td>TrB, TeB</td>
<td>38, 30, 22</td>
</tr>
<tr>
<td>Abundance isoprene emitters</td>
<td>%</td>
<td></td>
<td>↑ L</td>
<td>TrB</td>
<td>49</td>
</tr>
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Table 1 (Continued)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Symbol</th>
<th>Units</th>
<th>Response 1</th>
<th>Forest type(s)2</th>
<th>Reference(s)3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isoprene emission rate</td>
<td>I</td>
<td>nmol m⁻² s⁻¹</td>
<td>↑ H (peak in mid-canopy)</td>
<td>TrB</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ H</td>
<td>TeB</td>
<td>32, 60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↑ L</td>
<td>TeB</td>
<td>32, 61, 62</td>
</tr>
<tr>
<td>Monoterpene emission rate</td>
<td>MT</td>
<td>µg m⁻² s⁻¹</td>
<td>↑ H (peak in mid-canopy)</td>
<td>TeB</td>
<td>63</td>
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<tr>
<td>Thermal tolerance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photosynthetic heat tolerance</td>
<td>Tₛₒ₂</td>
<td>°C</td>
<td>↓ H</td>
<td>TrS</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>53, 54</td>
</tr>
<tr>
<td>Critical temperature beyond which Fₒ/Fᵣ declines</td>
<td>Tₒᵣ</td>
<td>°C</td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>53</td>
</tr>
<tr>
<td>Phenology</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Budbreak</td>
<td></td>
<td>day of year</td>
<td>↓ H</td>
<td>TeB</td>
<td>56</td>
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<tr>
<td>Leaf life span</td>
<td></td>
<td>months</td>
<td>↓ H</td>
<td>TeB</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>↓ L</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought deciduous leaf habit</td>
<td></td>
<td>%</td>
<td>↑ H</td>
<td>TrB</td>
<td>58, 59</td>
</tr>
</tbody>
</table>

Studies listed here were compiled using a systematic review process, as described in Supporting Information Methods S3.

1Responses across height and light gradients are summarized, with up and down arrows indicating significant increasing or decreasing trends, respectively, in response to height (H) or light (L). ⇒ indicates lack of any notable directional variation, and ⇒ ↑ or ⇑ − ↓ indicate nonsignificant or mixed trends (e.g. significant in some but not all species studied).
2Forest types are coded as follows: TrB, tropical broadleaf; TeB, temperate broadleaf; TeN, temperate needleleaf (conifer); BoN, boreal needleleaf (conifer); TrS, tropical savanna.

*Composite climatic stress variable integrating temperature, vapor pressure deficit, and relative humidity is higher in lower canopy.

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responsible for pine scent, light-dependent emissions are linked to photosynthetic substrate supply and are dynamically tuned to environmental and metabolic conditions as a component of metabolic regulatory processes (Laathawornkrit et al., 2009; Riedlmeier et al., 2017; Lautze et al., 2019; Monson et al., 2021). Due to its much higher emission rate and relative ease of detectability, isoprene has received far more study in the field, although both isoprene and monoterpenes are expressed by many angiosperms and gymnosperms across all biomes (see Taylor et al., 2021, and references therein).

Fewer than half of tree species express significant light-dependent isoprene emissions (Kesselmeier & Staudt, 1999; Taylor et al., 2018), such that vertical variation in emissions is influenced by both vertical variation in species compositions and by plasticity in emission rate capacities (Taylor et al., 2021). Within species, isoprene emission tends to increase toward brighter and hotter microenvironments (Niinemets, 2007), and across landscapes, emitting species are more abundant in hotter climates, the canopy surface (Table 1; Šimpraga et al., 2013). This pattern may indicate the importance of temporal variability in thermal conditions as distinct from the long-term average. Temperature-sensitive VOC emissions have been hypothesized to enable real-time acclimation to rapidly changing leaf thermal environments typical of the midcanopy region (Section II.1; Sharkey et al., 2008). Future work to understand how thermal dynamics of Tleaf vary with height and influence leaf function will be important for resolving the role of VOCs in forest thermal sensitivity across the vertical gradient. Given current understanding, we may hypothesize that light-dependent VOC emissions are important for midcanopy thermal responses, while other traits play similar roles in upper canopy leaves.

**Thermal tolerance** Very high Tleaf (c. 40–60°C) irreversibly damages photosystem II, leading to leaf necrosis and death (Baker, 2008; Feeley et al., 2020; Kunert et al., 2022). Upper thermal thresholds for leaf survival can be imitated by assessing the photosystem II functioning via using chlorophyll fluorescence techniques (Krause et al., 2010). Thermal tolerance is described in terms of the Tcrit at which photosystem II efficiency starts to decrease (Tcrit) and is reduced by 50%, Tₓ₀ (Slot et al., 2021a). Thermal tolerances vary across species, being more closely linked to leaf traits than phylogeny (Feeley et al., 2020; Slot et al., 2021a),
and being greater in leaves that experience higher maximum temperatures (Perez & Feeley, 2020). $T_{s_{0}}$ and $T_{air}$ decrease across increasing latitudes, and with elevation among tropical forests (O’Sullivan et al., 2017; Feeley et al., 2020; Slot et al., 2021a). However, they appear more closely adapted to microclimate than macroclimate (Feeley et al., 2020; Slot et al., 2021a).

Thermal tolerance is hypothesized to be greatest for the leaves with the greatest radiation loads and highest temperatures along the vertical gradient. Indeed, considering sun and shade leaf differences across the vertical profile of a closed-canopy forest in Panama, $T_{s_{0}}$ was 0.7°C–1.4°C lower for shade than sun leaves for two of three tree species (Table 1; Slot et al., 2019). Similarly, within a very open Acacia papyrocarpa canopy, $T_{s_{0}}$ was highest (albeit by <1°C) in the lower, north-facing leaves, which faced the greatest composite climate stress (low wind speed, greater radiation and $T_{air}$, and lower rates of heat dissipation) (Table 1; Curtis et al., 2019). These modest differences in $T_{s_{0}}$ coupled with larger differences in $T_{leaf}$ across thermal microenvironments imply that more thermally tolerant sun leaves tend to operate closer to their thermal limits and could therefore be more vulnerable to heat anomalies (Perez & Feeley, 2020). However, not enough studies have evaluated thermal tolerances across vertical gradients to make robust inferences.

**Leaf phenology** Leaf phenology influences the vertical structure of microenvironments, $T_{leaf}$, and forest photosynthetic capacity (Rey-Sánchez et al., 2016). In deciduous forests, the timing and extent of seasonal leaf gain and loss is structured across the vertical profile. In temperate climates, seasonal warming occurs earlier in the sheltered understory, facilitating earlier spring budbreak compared with the cooler upper canopy (Augspurger & Bartlett, 2003). Early leaf-out gives saplings and seedlings a sheltered understory, facilitating earlier spring budbreak and extent of seasonal leaf gain and loss is structured across the vertical profile of a closed-canopy forest in Panama, $T_{s_{0}}$ was 0.7°C–1.4°C lower for shade than sun leaves for two of three tree species (Table 1; Slot et al., 2019). Similarly, within a very open Acacia papyrocarpa canopy, $T_{s_{0}}$ was highest (albeit by <1°C) in the lower, north-facing leaves, which faced the greatest composite climate stress (low wind speed, greater radiation and $T_{air}$, and lower rates of heat dissipation) (Table 1; Curtis et al., 2019). These modest differences in $T_{s_{0}}$ coupled with larger differences in $T_{leaf}$ across thermal microenvironments imply that more thermally tolerant sun leaves tend to operate closer to their thermal limits and could therefore be more vulnerable to heat anomalies (Perez & Feeley, 2020). However, not enough studies have evaluated thermal tolerances across vertical gradients to make robust inferences.

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4. **Leaf gas exchange and its thermal sensitivity** Leaf gas exchange is strongly shaped by environmental drivers, $T_{leaf}$ and traits, all of which vary across vertical forest gradients (Sections II.1–II.3; Fig. 1). However, as we detail below, few studies have evaluated how temperature responses of leaf metabolic rates are shaped by the varying environmental conditions across vertical forest gradients (Table 2).

**Conductance** Leaf hydraulic, stomatal, and boundary layer conductances are all critical for regulating $T_{leaf}$ via latent heat loss (Fig. 3). Due to higher wind, lower RH, and smaller leaf sizes in the upper canopy (Fig. 2; Table 1), $g_{s}$ increases with height (Table 2). Maximum $g_{s}$ increases with light – typically tracking photosynthetic capacity (Wong et al., 1979) – and is thus higher in the sun-exposed upper canopy than in subcanopy or understory leaves (Table 2). However, water supply cannot meet the demands caused by the high radiation and $g_{s}$ in sun leaves with fully open stomata, in part because of height-related constraints on water transport (Yoder et al., 1994; Koch et al., 2004; Sillett et al., 2010) and/or increased leaf-air VPD caused by leaf warming in sunlit canopy locations (Buckley et al., 2014). These constraints tend to reduce leaf water potential, making midday stomatal depression more prevalent in sun leaves than shade leaves in closed-canopy forests (Table 2), which drives the lower intracellular CO₂ and δ¹³C (see Section II.3 subsection ‘Metabolic capacity and efficiency’; Table 1). Stomatal depression reduces transpirational cooling (Fig. 3e), thus amplifying the warming of sun leaves by high radiation (Koch et al., 1994; Zwieniecki et al., 2004; Kosugi & Matsuo, 2006; Sanches et al., 2010). The temperature at which $g_{s}$ is greatest, $T_{opt}$ of $g_{s}$, did not differ significantly between sun and shade leaves in three tropical tree species (Slot et al., 2019), but sun leaves in the upper canopy show a stronger decrease in $g_{s}$ in response to rising $T_{air}$ (driven by increased VPD) than lower canopy shade leaves (Hernández et al., 2020; Carter et al., 2021). Available data also suggest that high $T_{air}$ can directly drive stomatal opening, if vapor pressure is experimentally adjusted in tandem with $T_{air}$ to keep VPD constant (Fredeen & Sage, 1999; Mott & Peak, 2010; Urban et al., 2017), although it appears that the negative effect of temperature on $g_{s}$, mediated by VPD, generally overrides the positive effect of temperature per se in nature, causing $g_{s}$ to decline when the leaf warms.

**Photosynthesis** Photosynthetic capacity is generally higher in exposed canopy positions – a fact that is both predicted by optimization theory (Field, 1983; Hirose & Werger, 1987) and observed in numerous field studies (Table 2).

Temperature can affect photosynthesis directly, by altering photosynthetic enzyme activity and the electron transport chain, and indirectly, by increasing VPD and closing stomata (Lloyd & Farquhar, 2008). Photosynthesis has a peaked response to $T_{air}$ with the optimum commonly corresponding to the prevalent ambient growing season temperature (Doughty & Goulden, 2008; Slot & Winter, 2017; Tan et al., 2017). Beyond the optimum, photosynthesis decreases due to stomatal closure (Slot & Winter, 2017; Grossiord et al., 2020; Smith et al., 2020) and biochemical...
Table 2 Summary of observed variation in leaf gas exchange and its thermal sensitivity across the vertical gradient and/or between sun and shade leaves.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Symbol</th>
<th>Units</th>
<th>Response</th>
<th>Forest type(s)$^2$</th>
<th>Reference(s)$^3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conductance</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Boundary layer conductance</td>
<td>$g_o$</td>
<td>mmol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>14, 11, 15, 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mm s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeN</td>
<td>16</td>
</tr>
<tr>
<td>Leaf hydraulic conductance</td>
<td>$K_{\text{leaf}}$</td>
<td>m$^{-2}$ s$^{-1}$ MPa$^{-1}$</td>
<td>↑ L</td>
<td>TeB, BoN</td>
<td>1, 2</td>
</tr>
<tr>
<td>Cuticle conductance</td>
<td>$g_{\text{min}}$</td>
<td>mmol m$^{-2}$ s$^{-1}$</td>
<td>↑ L</td>
<td>TrB</td>
<td>38</td>
</tr>
<tr>
<td>Max stomatal conductance</td>
<td>$g_{\text{max}}$</td>
<td>mol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>8, 9, 10, 7, 4</td>
</tr>
<tr>
<td>Stomatal conductance limitation</td>
<td>$g_s$</td>
<td>mol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeN</td>
<td>9, 39, 5, 6, 7</td>
</tr>
<tr>
<td>Stomatal conductance at optimal temperature</td>
<td>$g_s$ at $T_{\text{opt}}$</td>
<td>mol m$^{-2}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeB, BoN</td>
<td>9, 39, 7, 27</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Maximum photosynthetic capacity</td>
<td>$A_{\text{max}}$</td>
<td>mol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>14, 11, 15, 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nmol g$^{-1}$ s$^{-1}$</td>
<td>↓ H</td>
<td>TrB, TeB, BoN</td>
<td>16</td>
</tr>
<tr>
<td>Maximum light-saturated net photosynthesis</td>
<td>$A_{\text{sat}}$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ L</td>
<td>TrB, TeB</td>
<td>21, 22</td>
</tr>
<tr>
<td>$A_{\text{sat}}$ at optimum temperature</td>
<td>$A_{\text{opt}}$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ ↑ L</td>
<td>TrB, TeB</td>
<td>13, 11</td>
</tr>
<tr>
<td>Optimum temperature for photosynthesis</td>
<td>$T_{\text{opt}}$</td>
<td>°C</td>
<td>≈ ↑ H</td>
<td>TrB, TeB</td>
<td>23, 11, 13</td>
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<td></td>
<td></td>
<td></td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>39</td>
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<tr>
<td>Photosynthetic light compensation point</td>
<td>LCP</td>
<td>μmol m$^{-2}$</td>
<td>↑ H</td>
<td>TrB, TeB, TeN</td>
<td>24, 16</td>
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<tr>
<td>Maximal carboxylation rate</td>
<td>$V_{\text{cmax}}$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ L</td>
<td>TrB, TeB, BoN</td>
<td>2, 39, 22, 14</td>
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<tr>
<td></td>
<td></td>
<td>nmol g$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ H</td>
<td>TrB, TeB, BoN</td>
<td>9, 39, 22, 14</td>
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<td>Optimum temperature for $V_{\text{cmax}}$</td>
<td>$V_{\text{cmax}}$ (T$_{\text{opt}}$)</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>≈ ↑ H</td>
<td>TrB, TeB</td>
<td>25</td>
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<tr>
<td>Electron transport rate</td>
<td>$J_{\text{max}}$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ L</td>
<td>TrB, TeB</td>
<td>2, 39, 22, 14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nmol g$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>9, 39, 22, 16</td>
</tr>
<tr>
<td>Optimal temperature of $J_{\text{max}}$</td>
<td>$T_{\text{ETR opt}}$</td>
<td>°C</td>
<td>≈ ↑ H</td>
<td>TrB, TeB</td>
<td>22</td>
</tr>
<tr>
<td>High-temperature CO$_2$ compensation point</td>
<td>$T_{\text{max opt}}$</td>
<td>°C</td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>22</td>
</tr>
<tr>
<td>Respiration</td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Respiration rate at 25°C</td>
<td>$R$</td>
<td>μmol CO$_2$ m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB, TeN</td>
<td>36, 28, 29, 30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>μmol CO$_2$ kg$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeB, TeN</td>
<td>28, 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>μmol CO$_2$ kg m$^{-2}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeN</td>
<td>28, 30</td>
</tr>
<tr>
<td>Light respiration</td>
<td>$R_L$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB</td>
<td>21</td>
</tr>
<tr>
<td>Dark respiration</td>
<td>$R_{\text{dark}}$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>↑ H</td>
<td>TrB, TeB, BoN</td>
<td>21, 14, 31, 22, 38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>nmol g$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ H</td>
<td>TrB, TeB, TeN, BoN</td>
<td>21, 14, 22, 17, 10, 35</td>
</tr>
<tr>
<td>$R_{\text{dark}}$ at reference $T$</td>
<td>$R_{\text{dark}}$ at reference $T$</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeB, BoN</td>
<td>2, 32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>μmol (kg leaf)$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ H</td>
<td>TrB, TeB, TeN</td>
<td>21, 14, 31, 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>μmol (kg N)$^{-1}$ s$^{-1}$</td>
<td>≈ ↑ H</td>
<td>TeB, TeN</td>
<td>3, 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>≈ ↑ L</td>
<td>TrB, TeB</td>
<td>2, 8, 34</td>
</tr>
</tbody>
</table>
Table 2 (Continued)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Symbol</th>
<th>Units</th>
<th>Response</th>
<th>Forest type(s)</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature sensitivity of R&lt;sub&gt;dark&lt;/sub&gt;</td>
<td>Q&lt;sub&gt;10&lt;/sub&gt;</td>
<td>°C&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>≈ H</td>
<td>TrB, TeB, TeN</td>
<td>21, 36, 31, 30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>°C&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>≈ L</td>
<td>TeB, TeN</td>
<td>3, 29</td>
</tr>
<tr>
<td>Activation energy of R&lt;sub&gt;dark&lt;/sub&gt;</td>
<td>E&lt;sub&gt;0&lt;/sub&gt;</td>
<td>kJ mol&lt;sup&gt;-1&lt;/sup&gt; K&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>≈ H</td>
<td>TrB, TeB, TeN</td>
<td>21, 34, 29</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>≈ L</td>
<td>TrB</td>
<td>21, 8</td>
</tr>
</tbody>
</table>

Studies listed here were compiled using a systematic review process, as described in Supporting Information Methods S3.

Responses across height and light gradients are summarized, with up and down arrows indicating significant increasing or decreasing trends, respectively, in response to height (H) or light (L). ≈ indicates lack of any notable directional variation, and ≈ ↑ or ≈ ↓ indicate nonsignificant or mixed trends (e.g. significant in some but not all species studied).

Forest types are coded as follows: TrB, tropical broadleaf; TeB, temperate broadleaf; TeN, temperate needleleaf (conifer); BoN, boreal needleleaf (conifer).

**Constraint**: (Sharkey, 2005; Várhammar et al., 2015; Kumarathunge et al., 2019).

We have very little evidence about how the temperature sensitivity of photosynthesis compares between sun and shade leaves, and existing studies, which compare sun and shade leaves of the same trees, reveal no pronounced overall trend with height in photosynthetic temperature optima (Table 2). Based on consistent positive relationships between growth temperature and optimum temperature of photosynthesis (T<sub>opt</sub>) across sites and seasons (Tan et al., 2017; Kumarathunge et al., 2019), one might expect sun leaves to have a stronger temperature dependence and higher T<sub>opt</sub> than shade leaves (Campbell & Norman, 1998; Niinemets et al., 1999; Niinemets & Valladares, 2004). However, such a trend is not apparent among recent studies, where for three species in Panama, T<sub>opt</sub> for sun leaves tended to be moderately, but not significantly, higher than that of shade leaves (Slot et al., 2019; Hernández et al., 2020). Similarly, T<sub>opt</sub> of RuBP carboxylation (V<sub>max</sub>) and regeneration rates (J<sub>max</sub>) did not differ systematically between tropical sun and shade leaves (Hernández et al., 2020), nor within-canopies of tropical and temperate trees (Mau et al., 2018; Miller et al., 2021). By contrast, tropical experimental warming observations showed that T<sub>opt</sub> and T<sub>opt</sub> of J<sub>max</sub> decrease from the understory to the top of the canopy, potentially linked to greater thermal sensitivity of g<sub>i</sub> in upper canopy leaves (Carter et al., 2021). The observed lack of sun–shade differences in T<sub>opt</sub> may reflect acclimation to similar temperatures of peak photosynthesis (Hernández et al., 2020). Sun leaves experience higher temperatures, but maximum temperatures are associated with conditions of midday stomatal depression, and acclimation to optimize photosynthesis at these temperatures would not be advantageous. Shade leaves that do not experience midday depression continue to fix carbon even when afternoon air temperatures peak (Miller et al., 2021). Evaluating this would require diurnal monitoring of net photosynthesis across a forest vertical profile. In the meantime, it remains unresolved whether photosynthesis is more affected by high temperatures in upper canopy or understory leaves, and how this might vary across forest types and environmental conditions.

**Respiration** Similar to photosynthesis, respiration tends to be higher in upper canopy sun leaves, but its temperature sensitivity (Q<sub>10</sub> or E<sub>0</sub>) shows no definite trend along the vertical gradient. Specifically, the temperature sensitivity of respiration can be constant within vertical profiles and in seedling sun vs shade leaves, greater in upper canopy leaves, or greater in the lower canopy (Table 2). This variation may be attributable to forest type, leaf traits, and age (e.g. greater Q<sub>10</sub> in younger leaves; Zhou et al., 2020), or aclimation to high temperature that decreases Q<sub>10</sub> (Slot & Kitajima, 2015; Carter et al., 2021). Overall, although the temperature difference between upper and lower canopy positions is an important driver of respiration, we currently lack mechanistic understanding of how and why its temperature sensitivity varies across the forest vertical profile.

**5. Tree and ecosystem ecology**

Differences across forest vertical gradients in biophysical conditions, plant traits, and metabolism scale up to affect ecological rates and their temperature responses at tree and ecosystem levels (Fig. 1).

Tree metabolism, growth, and survival** Tree metabolism and growth are shaped by crown location in the vertical gradient. Tree height, crown volume, and foliage biomass all scale with diameter at breast height (DBH), which strongly predicts tree transpiration (Meinzer et al., 2001; Anderson-Teixeira et al., 2015; Kunert et al., 2017) photosynthesis, and intracanopy trait variation (Bin et al., 2022). Specifically, increases are linked to greater leaf area and the increasing probability that the crown is in the canopy (Muller-Landau et al., 2006), where leaves receive more light and have higher leaf area-specific photosynthesis (Table 2). Photosynthes
production is allocated among functions including respiration, aboveground woody growth, foliar turnover, root growth and allocation to root-associated microorganisms, reproduction, defense, and storage of nonstructural carbohydrates (NSCs). Among these, the best-studied process is aboveground woody growth, which consumes only a modest fraction of total photosynthetic carbon (c. 1/6 on the ecosystem level; Anderson-Teixeira et al., 2021), but is critically important to long-term forest dynamics and carbon cycling because woody tissues have a long residence time in the ecosystem (Russell et al., 2014). Radial stem growth may increase or decrease over time as trees grow in DBH depending on the light environment (Anderson-Teixeira et al., 2022). In open forests and for open-growth individual trees, growth rate declines with DBH, whereas growth rate consistently increases with DBH for trees established in the understory of a closed-canopy forest (Muller-Landau et al., 2006; Anderson-Teixeira et al., 2015, 2022). This points to a dominant role of vertical profiles in the biophysical environment, particularly light, in shaping tree growth rates within forests.

Vertical gradients also affect the climate sensitivity of metabolism and growth. Stomatal conductance can be strongly limited by high VPD even when soil water is plentiful (Corlett, 2011; Novick et al., 2016; Ruehr et al., 2016). Therefore, periods of high VPD, whether on timescales of hours, days, or seasons, tend to reduce transpiration and photosynthesis more in tall trees that occupy canopy positions in closed-canopy forests (Christoffersen et al., 2016; García et al., 2021). This is consistent with observations that both dry season leaf loss (see Section II.3 subsection ‘Leaf phenology’; Table 1) and g limitation (see Section II.4 subsection ‘Conductance’; Table 2) increase with height across the vertical profile. More active regulation of transpiration by tall canopy trees (Mediavilla & Escudero, 2004)—often combined with greater effective rooting depth—may offset greater xylem embolism risk (Olson et al., 2018; Chiitra-Tarak et al., 2021; García et al., 2021)—and reduce the need to adjust carbon metabolism traits during drought (Bartholomew et al., 2020). This reduces carbon isotope discrimination, indicative of greater g limitation, with increasing tree height (Table 1; McDowell et al., 2011).

In turn, the drought sensitivity of woody growth tends to be greater in upper canopy trees than in smaller trees with less exposed crowns. dendrochronologists generally agree that tree ring records of large, exposed trees are best suited for climate reconstructions because their annual growth is most sensitive to interannual climate variation (Fritts, 1976). However, few studies have directly examined drought- or temperature sensitivities as a function of tree size. Most have found greater sensitivity to low precipitation or seasonally high temperatures among larger, more exposed trees (Fig. 4; Trouullier et al., 2018; Gillerot et al., 2020; McGregor et al., 2021; Anderson-Teixeira et al., 2022; Heilman et al., 2022), corroborating evidence from global forest censuses that drought reduces growth more in large trees (Bennett et al., 2015). Drought also causes greater mortality in larger trees (Bennett et al., 2015; Stovall et al., 2019). Mechanistically, this is likely driven in part by larger trees having their crowns in microenvironments that are more challenging during drought (Figs 1–3; Scharweber et al., 2019), yet height itself also creates disadvantages (Couvreur et al., 2018; Olson et al., 2018). Indeed, despite the potential for shorter trees in open forests to experience greater environmental stress (Curts et al., 2019), greater drought sensitivity of larger trees has been observed in open and closed-canopy forests (Bennett et al., 2015; Anderson-Teixeira et al., 2022). However, evidence that short trees in young stands can be more drought-sensitive than taller trees in mature forests (Irvine et al., 2004; Wang et al., 2022) reinforces the importance of exposure in shaping drought sensitivity. The relative importance of exposure vs height in shaping drought sensitivity remains to be disentangled.

Although drought sensitivity clearly increases with crown height and hence with DBH, it remains unclear how growth sensitivity to high Tair, independent of drought, varies along the vertical gradient. High Tair is often associated with high VPD and atmospheric drought, likely explaining negative growth responses to Tair—particularly among larger trees—even if soil moisture remains high (Novick et al., 2016), or when precipitation is statistically accounted for (Fig. 4; Anderson-Teixeira et al., 2022). However, under well-watered conditions conducive to high g, we do not necessarily expect higher thermal sensitivity of photosynthesis (see Section II.4 subsection ‘Photosynthesis’) or woody growth in upper canopy trees than their understory counterparts. Indeed, there are cases where tree ring records show more negative or less positive Tair–responses of understory trees than canopy dominants (Rollinson et al., 2020; Anderson-Teixeira et al., 2022). Additional research is required to understand the mechanisms underlying these intriguing differences, and to disentangle size-related tree growth responses to hot-wet vs hot-dry conditions.

**Carbon and water flux** Canopy trees account for the majority of forest ecosystem water and carbon cycling. While studies partitioning transpiration across forest vertical gradients are rare, both evapotranspiration (ET) and transpiration have been shown to increase with height in a *Pinus abies* forest in Germany, where the upper half of the canopy contributed an estimated 80% of daytime ET (Staudt et al., 2011). Similarly, in a tropical forest in the Brazilian Amazon, canopy and subcanopy trees jointly contributed c. 93% of ET, or 88% of transpiration (Fig 5a; Kunert et al., 2017), and trees > 33 cm DBH contributed > 80% of transpiration in a forest in Costa Rica (Moose et al., 2018). In terms of carbon cycling, it has been estimated that the canopy strata contribute ≥ 64% of net daytime CO2 uptake (i.e. gross primary productivity (GPP) – ecosystem respiration, including from soil; Misson et al., 2007). Large trees also dominate woody aboveground net primary productivity (ANPPwoody) and mortality (Mwoody), with trees ≥ 10 cm DBH usually contributing > 85% of ANPPwoody and Mwoody across 25 globally distributed forests (Fig. 5b; Piponi et al., 2022).

It is less clear how thermal sensitivity of water and carbon fluxes vary across strata, but probable responses can be inferred based on the patterns and mechanisms reviewed above. We expect that under conditions of moderate-to-high VPD, transpiration, GPP, and ANPPwoody should all be more sensitive to high temperatures in the upper canopy than in the understory (Grossiord et al., 2020; Nunes et al., 2022). Because canopy trees dominate these fluxes (Fig. 5), their responses will strongly influence the whole-ecosystem response, potentially with modest buffering by the understory.
Thus, for example, increases in canopy temperature reduce forest GPP in the tropics (Pau et al., 2018). Yet, evidence also suggests GPP and ecosystem respiration are less sensitive to heat and drought stress in older forests than in young forests (Xu et al., 2020), perhaps in part because of more complex vertical structuring (Jones et al., 2019; Nunes et al., 2022). A rare example of a study comparing climate sensitivity of C fluxes across size classes (Meakem et al., 2018) showed that $M_D$ was more strongly elevated among large than small trees during an El Niño drought in Panama, while the smallest trees had higher productivity during the drought, likely because of increased light in the understory. It remains far less clear how thermal sensitivity varies across forest strata under wet conditions, but both physiological mechanisms (Fig. 3) and some tree ring evidence (Rollinson et al., 2020; Anderson-Teixeira et al., 2022) raise the possibility that understory trees may be at a relative disadvantage under hot, humid conditions. Further research is required to better understand the thermal sensitivity of forest ecosystem function across strata.

III. Implications

Having established how physical conditions and biological form and function vary across vertical gradients (Fig. 1), we now turn to the implications of these patterns for understanding how forest ecosystems may be impacted by global change, and our ability to project this across space and time.

1. Global change responses

The complex interwoven relations between the biophysical environment and biological factors—leaf traits, metabolic processes, and distribution of species across forest strata—are likely to produce amplifications and feedback loops in a warming world, with implications for forests on many levels.

Warming As climate change progresses, we anticipate increases in both mean daytime and nighttime $T_{air}$ as well as increased maximum temperatures, with extreme increases during heat waves (IPCC, 2021). To the extent that warming is coupled with drought, we expect that tall trees with exposed crowns will usually be hardest-hit, particularly in severe drought, partly because their crowns are positioned in a more challenging microenvironment (see Section II.5 subsection ‘Tree metabolism, growth, and survival’; Figs 1–4). By contrast, understory trees will be more sheltered during droughts and heat waves, and in some settings may benefit from increased light availability (Bennett et al., 2015; Hogan et al., 2019; Nunes et al., 2022). It remains unclear how these patterns vary with the nature of the drought, including the relative contributions to stress from low soil moisture vs high VPD. While the two are coupled over longer timescales (Novick et al., 2016; Humphrey et al., 2021), the latter can be intense for short periods even when soil moisture is high (e.g. during a heat wave) and exerts a stronger influence on ET in many biomes (Novick et al., 2016). Given the mechanisms reviewed here, we might expect that high VPD in particular skews the stress more toward the exposed canopy trees.

It remains uncertain how responses to warming will vary across vertical gradients under mesic conditions. Leaves display substantial plasticity to adapt to warmer temperatures (Cunningham & Read, 2003; Way, 2019; Slot et al., 2021) and to recover from heat stress (Smith et al., 2020), yet failure to fully acclimate will reduce carbon sequestration at leaf, tree, and ecosystem levels (Tan...
As growing season $T_{air}$ increasingly equals or exceeds photosynthetic optima (Slot & Winter, 2017; Mau et al., 2018; Huang et al., 2019; Kumarathunge et al., 2019), exposed crowns are likely to be most vulnerable. Particularly in midlatitude forests, which have the narrowest thermal safety margin between historical maximum temperatures and $T_{crit}$ (O’Sullivan et al., 2017), $T_{leaf}$ of sun-exposed leaves may approach tolerance thresholds during heat waves, causing photosynthetic decline or even leaf death (O’Sullivan et al., 2017; Tiwari et al., 2021; Kunert et al., 2022). By contrast, understory leaves and trees are unlikely to face the same absolute extremes of $T_{leaf}$ and protection from thermal stress.

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### Fig. 5 Vertical partitioning of (a) evapotranspiration and (b) carbon fluxes in tropical forests.

Panel (a) is from Kunert et al. (2017); (b) presents averages for 14 tropical forests from Piponiot et al. (2022). DBH, diameter at breast height; ANPP, aboveground net primary productivity; $M_{woody}$, woody mortality.

<table>
<thead>
<tr>
<th>Size of DBH Trees</th>
<th>ANPP $\text{woody}$</th>
<th>$M_{woody}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\geq 60$ cm DBH trees</td>
<td>28% (3–61%)</td>
<td>36% (11–54%)</td>
</tr>
<tr>
<td>10–60 cm DBH trees</td>
<td>63% (34–82%)</td>
<td>57% (39–82%)</td>
</tr>
<tr>
<td>$&lt; 10$ cm DBH trees</td>
<td>9% (1–15%)</td>
<td>7% (2–15%)</td>
</tr>
</tbody>
</table>
associated with high direct radiation might allow shaded layers to photosynthesize longer in the day (He et al., 2018; Miller et al., 2021). However, with $T_{air}$ more frequently equalling or exceeding photosynthetic optima, occasional exposure to sunlight coupled with lower capacity to dissipate excess heat may prove disadvantageous. While it is currently difficult to predict whether canopy or understory photosynthesis will be more severely affected by warming (see Section II.4 subsection ‘Photosynthesis’), limited tree ring evidence indicates that unusually hot growing seasons can dramatically reduce the growth of understory trees (Rollinson et al., 2020), and these small trees may be at higher risk of carbon starvation because they have lower NSC reserves (Niinemets, 2010). Thus, despite their buffered microclimate, it is possible that understory trees could be more adversely impacted by warming temperatures than their canopy counterparts under some conditions.

Canopy disturbance Increasing severity and frequency of heat waves, accompanied with increases in VPD and ET, places canopy trees at particularly elevated risk of mortality (see Section II.5 subsection ‘Tree metabolism, growth, and survival’), potentially causing large-scale canopy dieback (Matusick et al., 2013; Teskey et al., 2015; Breshears et al., 2021). Large trees are also the most vulnerable to other climate-related disturbances (e.g. wind and lightning; Gora & Esquivel-Muelbert, 2021) that are expected to intensify with climate change (IPCC, 2021), and they are also targeted by selective logging (Miller et al., 2011). Forest fragmentation also kills large trees by making them more vulnerable to wind, desiccation, and liana infestation (Laurance et al., 2006). Thus, canopies are becoming increasingly prone to disturbance and gap formation, which in turn increases radiation and temperatures within the forest (Jucker et al., 2018; Stark et al., 2020). Such changes often enhance growth of smaller trees, which benefit from increased light (Bennett et al., 2015; Hogan et al., 2019; Nunes et al., 2022), and wetter forests can prove quite resilient to canopy disturbance (Miller et al., 2011). However, this shift to hotter and drier microclimates makes some forests more susceptible to further disturbances, for example, increasing fire risk (Brando et al., 2014; Aragão et al., 2018). Severe degradation can cause dramatic ecological state changes (e.g. the transition of tropical forests to more open, savanna-like vegetation) and nonlinear threshold responses in energy balance and associated microclimates, with implications for forest–atmosphere interactions (Stark et al., 2020).

Such dynamics are likely to be amplified by warming, such that climate change is pushing some of the world’s forests into alternative stable states wherein forest can persist as long as the climate change is pushing some of the world’s forests into alternative stable states wherein forest can persist as long as the ecosystem-level resilience to canopy disturbance that is often provided by smaller trees (Miller et al., 2011) will be destroyed, resulting in breakdown of canopy structure and the potential state changes described above.

2. Scaling across space and time

As we have reviewed here, vertical profiles in forests strongly shape forest dynamics and climate change responses. Ultimately, to achieve the important goal of understanding feedback between the world’s forests and climate change, these mechanisms must be sufficiently represented in models and scaled spatially via remote sensing.

Representing vertical gradients in models Dynamic global vegetation models (DGVMs), which comprise the land surface models in Earth system models, are used to predict the global distribution of vegetation types and biosphere–atmosphere feedback (Foley et al., 1996; Sitch et al., 2003; Woodward & Lomas, 2004). Dynamic global vegetation models operate at a range of scales and vary in complexity, from detailed individual-based models (i.e. forest gap models), which represent vegetation at the level of individual plants, capturing spatial variability in light environment and microclimates at high 3D spatial resolution (Shugart et al., 2018), to big-leaf models that reduce 3D vegetation structure to single vegetation layer, implicitly capturing vertical profiles in light, photosynthetic capacity and other features by assuming those profiles are exponential and thus can be integrated analytically (Bonn et al., 2003; Krinner et al., 2005). This simplification is computationally more efficient but does not always capture observed vertical profiles (Sections II.1–II.4; for example, vertical shifts in the balance between stomatal conductance and photosynthetic capacity, see Section II.4 subsections ‘Conductance’ and ‘Photosynthesis’) and cannot capture important demographic processes and vertical light competition (Hurtz et al., 1998; Smith et al., 2001; Krinner et al., 2005). The computational middle-ground lies in cohort-based models, which represent vegetation as cohorts of individuals, grouped together based on properties, including size, age, and functional type (Fisher et al., 2018).

Owing to differences in the representation of forest vertical strata, DGVMs vary in their capacity to incorporate vertical variation in leaf traits and physiological processes. In general, however, this variation is accounted for via light competition. Models partition radiation above and within the forest vertical profile (i.e. direct vs diffuse light) using radiative transfer models or a system of two coupled ordinary differential equations, referred to as a two-stream imation (Sellers, 1985; Fisher et al., 2018). Using the latter method, single canopy layers are divided into sun and shade fractions (e.g. in the Community Land Model), while models with multiple vegetative layers can analytically solve the two-stream imation for each layer. Thus, even in single-layer models, key physiological parameters such as $V_{max}$ and $J_{max}$ vary, decreasing with increasing cumulative LAI or lower light conditions (Table 2;
Recent years have seen growing efforts to incorporate vertical variation more directly in models, specifically involving leaf water potential and light absorption, along with an increasing interest in confronting models directly with field measurements (Fisher & Koven, 2020; Maclean & Klinges, 2021). Recent model developments at the cutting edge of representing vertical variation (Bonan et al., 2018; Chen et al., 2019; Longo et al., 2019) implement vertical gradients of irradiance, water content, $T_{\text{leaf}}$, and humidification of canopy air by transpiration, modulated by turbulence within the forest and a roughness layer that extends to roughly twice the canopy height (Fisher & Koven, 2020).

The findings of this review reinforce the notion that representing vertical structuring is essential to capturing forest dynamics under global change. Improved representation of vertical variation in forest structure and ecosystem function is critical for representing thermal sensitivity and has repeatedly been identified as important for reducing uncertainty and accurately characterizing biologically mediated feedback (Moorcroft et al., 2001; Banerjee & Linn, 2018; Bonan et al., 2021). Moreover, given the anticipated importance of midcanopy and understory trees in ecosystem resilience and given the increasing mortality of canopy trees, it is essential that models separately represent these strata. A key question is whether existing models adequately represent the processes that underpin understory and large tree responses to thermal stress. Most models have been developed to capture dynamics in the upper canopy, given the disproportionate role of large trees in ecosystem dynamics (Fig. 5). Less attention has focused on developing and validating understory models.
tree dynamics and responses to perturbations in models, in large part to the paucity of observational and experimental studies needed to resolve key patterns and underlying mechanisms (Sections II.4, II.5). Pairing of models with observational studies is key to further improving our mechanistic understanding of vertical gradients and their implications.

Although an improvement over big-leaf models, DGVMs that separate the canopy into only two layers (e.g. sunlit and shaded portions; De Puru & Farquhar, 1997) may not be able to capture important within-canopy variation in terms of leaf dynamics (e.g. seasonal shifts in vertical leaf area distributions; Table 1; Smith et al., 2019) and functions (e.g. thermal responses; Table 2). Multilayered ecosystem models will likely be necessary for accurately predicting future forest function (Bonan et al., 2021). In addition, capturing vertical gradients in ET, GPP, respiration, and woody growth, and subsequently the net ecosystem effects, requires improved characterization of the functional response of leaf-level processes to vertically varying abiotic conditions, and the role of traits in mediating responses to thermal sensitivity.

**Scaling *in situ* data with remote sensing** Remote sensing data provide a valuable means to scale between *in situ* observations and DGVMs. Specifically, the increasing availability of airborne and spaceborne LiDAR and terrestrial remote sensing data offers a promising opportunity for mapping vertical thermal gradients and vegetation structure across scales (Fig. 6). Airborne, spaceborne, and terrestrial laser scanning data yield detailed 3D reconstructions of whole tree and forest structure. These data can be combined with thermal remote sensing data from the spaceborne ECOSTRESS sensor (Hulley et al., 2019; Fisher et al., 2020) or drone- and tower-based infrared cameras.

Detailed structural information from LiDAR data can be used to measure tree height, DBH, and crown dimensions (Fisher et al., 2020), evaluate spatial variation in vertical leaf area density profiles (Detto et al., 2015), and resolve complex seasonal and diurnal variation in shortwave radiation forcing in ecosystems (Musselman et al., 2013). Canopy shading can be better represented to predict understory temperatures by modeling the time-varying interaction of the forest canopy with solar radiation, as has been done in other LiDAR-based analyses (Davis et al., 2019). Satellite and airborne thermal infrared remote sensing analyses are now being conducted at regional and continental scales, although few applications exist at finer scales needed to understand vertical variation in canopy temperatures (Johnston et al., 2022). As an example of the type of insight possible with this approach, Pau et al. (2018) used the data from a tower-based infrared camera in combination with eddy-covariance data and found that tropical forest GPP was more strongly associated with canopy temperature than $T_{\text{air}}$ or VPD. In a savanna system in the Western USA, Johnston et al. (2022) found lower foliage temperatures at the tops of tree crowns than in the understory, which was influenced by very high grass temperatures, consistent with the principles outlined in Sections II.1 and II.2 (Fig. S1). The growing availability of such data makes this an opportune time to link *in situ* measurements to further explore ecosystem-scale patterns in vertical temperature gradients seasonally and across biomes.

**IV. Conclusions**

Across vertical gradients, directional trends in the biophysical environment and leaf traits are the rule, driving variation in the physiology and ecology that have these as their underpinnings (Fig. 1). However, uncertainty remains about how temperature sensitivity of foliar gas exchange varies across these vertical gradients. Similarly, much remains unknown about how crown exposure influences the temperature sensitivity of woody stem growth. While most available data suggest that large canopy trees are the most vulnerable to warming when water is limited, far less is known about the responses of understory trees.

As climate changes, patterns and processes across vertical gradients will likely shift as well. In the historical climates to which trees adapted, the canopy was an advantageous place for photosynthesis and growth. However, as temperatures increase, it is likely that exposed canopy positions will become increasingly physiologically stressful. ENSUANT increased mortality of canopy trees will create ever more gaps, changing understory conditions and community composition. Ultimately, mid- and understory tree communities will be critical to the resilience of forest ecosystems under changing climate, making improved understanding and model representation of their dynamics essential to understanding future forest dynamics. Integrating the patterns and mechanisms reviewed here, along with remote sensing data on forest structure and thermal environments, into cohort-based models that integrate with Earth system models will be crucial to understanding and forecasting forest–climate feedback in the coming decades.

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**Author contributions**

NV and KJA-T planned and designed the research, with contributions from all authors. NV reviewed the literature. NV, IRM, EMO and MNS contributed data and analyses. MS, TCT, LS and TNB contributed to writing and revising of the manuscript.

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Data availability

No new data were created in this study. New analyses are based on the data available from the National Ecological Observatory Network (NEON; https://www.neonscience.org/). The R scripts used for new analyses are available via GitHub (https://github.com/EcoClimLab/vertical-thermal-review) and archived in Zenodo (doi: 10.5281/zenodo.7050582).

References


Bonan GB, Patton EG, Finnigan JJ, Baldocchi DD, Harman IN. 2021. Moving beyond the incorrect but useful paradigm: reevaluating big-leaf and multilayer...


Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Vertical gradients in micrometeorological conditions for all forested sites in the National Ecological Observatory Network.

Methods S1 Methods for analyzing vertical gradients in the biophysical environment.

Methods S2 Methods for leaf energy balance modeling.

Methods S3 Methods for literature review.

Notes S1 Biophysical drivers of \( T_{\text{leaf}} \).

Table S1 National Ecological Observatory Network sites included in the analysis of vertical gradients of key biophysical characteristics.

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