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

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## Summary

*(currently too long for NewPhyt)*

Rising temperatures are expected to have profound effects on forests; however, it is not well understood how responses will vary across forest strata. Here, we synthesize evidence as to how environmental conditions and foliar traits vary across vertical gradients, shaping leaf temperatures, metabolism, and ultimately whole-tree growth and mortality. Strong vertical microclimatic gradients imply that canopy leaves are exposed to more solar radiation and higher evaporative demand than understory leaves, particularly in forests with dense canopies. However, foliar traits relevant to shaping leaf temperature () and metabolism also vary strongly across height or light gradients. Resulting ’s exceed air temperature () under conditions of high solar radiation, low wind, and low stomatal conductance. Differences are most pronounced when hydraulic limitations impede evaporative cooling such that ’s of sun-exposed canopy leaves become dramatically elevated above both and understory . While leaf metabolism generally increases with height across the vertical gradient, differences in thermal sensitivity, optimal temperatures, and thermal damage thresholds are modest. The implications for tree performance are mixed: whereas thermal buffering may contribute to the disproportionate stress of larger trees during drought, emerging tree-ring evidence suggests that understory trees experience relatively greater stress from high . Additional research will be important for improving our spotty understanding of the thermal sensitivity of metabolism and tree growth across vertical forest gradients. In the meantime, our findings imply that while large canopy trees are the most vulnerable to warming when combined with drought, understory trees may be more vulnerable under more mesic conditions.

## Introduction

Globally, temperatures have risen # C since YEAR and are expected to rise an additional #-#C by YEAR (IPCC REF). There is also increasing severity and frequency of heat waves that may potentially reduce [forest] biomass acculumation and disrupt photosynthesis and metabolic processes across plant species (O’Sullivan;REF ; Perkins *et al.*, 2012). These changes are expected to have profound effects on forest biodiversity and ecosystem function (REFS), and the resulting feedbacks to the climate system (e.g., decreased C storage, altered albedo and hydrology) will have a critical influence on the future of trajectory of climate change (Bonan, 2016, Bonan 2008).

**Rising temperatures are likely to have differential impacts on trees of different size and canopy position, in large part because small understory trees exist in a microenvironment that is substantially buffered by the more exposed canopy trees (Davis *et al.*, 2019; Zellweger *et al.*, 2019).**

Forests are vertically and horizontally stratified, with trees of different sizes through various successional stages. Overstory trees form canopies that play a crucial role in moderating macro-microclimate (Nakamura *et al.*, 2017; Ozanne *et al.*, 2003) by buffering extreme temperatures along with other macroclimatic conditions in the understory. This creates a vertical stratification of biophysical environments such as temperature, light, wind, humidity and Co2 which influences leaf temperature and metabolism along the gradient, and in turn whole plant performance [Bertrand et al. 2011].

The capacity of buffering largely depends on canopy cover and water availability (Davis *et al.*, 2019) each of which is subjected to change through climate-driven disturbances such as drought, deforestation, fire and related disruptions(Senf *et al.*, 2018). Increasing temperature has profound impacts on canopy cover such that temperate and tropical forest canopies are already or will soon be functioning beyond their optimal photosynthetic threshold (Mau *et al.*, 2018a; Huang *et al.*, 2019). Additionally, increased temperature is driving more frequent droughts causing hydraulic limitation in forests [ref]. Water limitation in forests alters species thermoregulation (Sastry *et al.*, 2018), also decreases tree canopy circumference (Aussenac, 2000) due to increased sensitivity of overstory to variability in water and precipitation (Rollinson *et al.*, p. 2020). Evidence shows that larger trees suffer hydraulic stress during drought [resulting in heat stressed canopy-leaves], which may contribute to increasing larger tree mortality in forests around the world should frequencies of drought continue to increase (McDowell *et al.*, 2008; Allen *et al.*, 2015, Brienen et al. 2015; Bennett *et al.*, 2015; Stovall *et al.*, 2019). Increases in loss of canopy cover (Senf *et al.*, 2018; Senf & Seidl, 2020) are also associated with reduced canopy structural complexity, altering microclimates with local heating effects and surface energy balance components (Stark *et al.*, 2020; Zellweger *et al.*, 2020a). However, in mesic forest conditions, availability of water enables canopies with suitable foliar traits to remain cool through continues evapotranspiration and consequential buffering of the understory [REF]

While forest microclimates are insulated from macroclimatic extremes, they are still experiencing warming trends (Bertrand *et al.*, 2020). As a result, understories experience a distinct set of pressures as microclimatic warming combines with conditions of limited light and related foliar traits, inter-species resource competition, etc. (Bartholomew *et al.*, 2020; Niinemets, 2010). Since temperature sensitivity is directly linked with plant metabolic processes and performance, even around 1 degree of warming can lead to changes in plant species composition and growth (Bertrand *et al.*, 2011, 2020). Plant communities in forest microclimates are already undergoing thermophilization (**???**; Zellweger *et al.*, 2019, 2020a; De Frenne *et al.*, 2013). Tree-ring evidence in mesic temperate forests shows reduced growth of understory trees relative to overstory with warming temperatures (Rollinson *et al.*, p. 2020). In addition, understory growth phenology is sensitive to warming year round, and especially in spring [Zohnner\_Renner 2019].

Microclimate warming has implications for forest regeneration (von Arx *et al.*, 2012). Temperature driven photosynthesis limitation is reducing tree growth rates, accompanying a global trend towards disturbed forests with younger trees (McDowell *et al.*, 2020). Reductions in canopy cover can lead to non-linear threshold responses, causing dramatic shifts from one forest state to another (e.g., transition from forest to savanna-like vegetation in tropical forest regions through “savannization”), with energy balance impacts and implications for forest-atmosphere interactions (Stark *et al.*, 2020). Each of these changes have potential feedbacks to climate change.

While there is evidence for temperature driven shifts in forest dynamics, leaf-level metabolic and performance changes influenced by biophysical conditions and warming in overstory and understory is still unclear. Thus, it is becoming more important than ever to understand foliage thermal sensitivity in forests along the vertical canopy profile, from the understory to the top of the canopy influenced by biophysical environmental gradient.This will provide crucial insights for how rising temperature affects forest ecology and biodiversity, energy balance, ecosystem function, and biosphere-atmosphere interactions [with additional feedbacks to forest structure and microclimates].

(Niinemets *et al.* (2004) highlights how biophysical and photosynthetic gradient varies along the vertical canopy profile, however our current knowledge of this topic is lacking.)

**We lack a systematic, up to date understanding of biophysical and biological patterns across the vertical canopy gradient in forests, how this gradient affects leaf-level processes, and in turn how it affects ecosystems (Fig. r fig\_schematic).**

**This review addresses the following questions:**

1. How does the biophysical environment vary with height in forests?
2. How do leaf traits vary with height (or between sun and shade leaves) in forests?(What types of leaf traits?-E.O)
3. How do vertical changes in biophysical environment conditions and leaf traits interact to affect leaf temperature [and in turn photosynthetic capacity]??
4. How does leaf metabolism respond to [air or leaf?] temperature in canopy and understory settings?
5. What are the implications of vertical canopy gradient patterns for the ecological and climate change responses of canopy versus understory trees?
6. What are the implications for modeling/ scaling / What are the implications of these leaf-scale responses at the ecosystem scale [in the context of climate change] / How do these leaf-level responses scale to entire ecosystems(*nerge these better*)

*Our primary interest is the gradient in height and exposure from the top of the canopy to the understory in forests. However, because a lot of the relevant research has focused on exposure gradients near ground level (e.g., comparisons of sun and shade leaves), and the implications [or utility] for ecosystem models we also review studies focused on exposure gradients.*



**Figure 1. (schematic of a forest summarizing most important gradients–sort of a “graphical abstract”.** Current version is just a very rough sketch of how this might look – needs to be filled in with content from the review. We could have a set of arrows for each of the major categories considered here. This would be a key figure, and should be beautifully illustrated—KAT could do a watercolor, or Nidhi could illustrate- and make use of NewPhyt’s figure editing service for Tansley reviews).

Martijn : in this illustration it would also be nice to show that you can have shade leaves of canopy trees in the understory, and shaded plants of understory species.

## The biophysical environment

The biophysical environment, here defined to include the physical structure of the forest canopy (from understory to the top of the canopy) and associated microclimates, is in large part determined by the structure of the forest itself. We supplement a review of the existing literature with a new analysis of data on vegetation structure and vertical microclimate profiles from the U.S. National Ecological Observatory Network [NEON; Appendix S1; Schimel et al. 2007].

Canopy foliage, which varies across forest types and seasonality, strongly shapes understory light, wind, etc. Forest canopies have a buffering effect on multiple aspects of the understory climate (Fig. 2).

* (*Bonan (2016) reviews this and points to appropriate references*)

*(paragraph on leaf area distribution, including figure (*[*separate from or combined with current Fig. 2- see GitHub issue #15*](https://github.com/EcoClimLab/vertical-thermal-review/issues/15)*)* The vertical structure and corresponding microenvironments of forest canopies vary seasonally (Parker & Tibbs 2004; Smith *et al.* (2019) ; Parker *et al.* (2019)) and following disturbance (e.g., Parker *et al.*, 2002 ; Stark *et al.*, 2020; Almeida *et al.*, 2016 ). In this review, we focus primarily on growing season conditions, including leaf phenology at the edges of the growing season, but excluding periods when no leaves are present in deciduous forests.

Light conditions, specifically changes in photosynthetically active radiation (PAR), vary along the vertical gradient with leaf area index (LAI), canopy height, canopy structure, and across species and forest types (Koike *et al.*, 2001). Generally, upper canopies in dense forests are exposed to greater PAR values and limit light penetration to canopy interiors, lower canopy layers, and the understory. Shaded regions experience lower values and quality of PAR [in ranges of blue, orange and red]. The light gradient is more pronounced under broadleaf forests than needleleaf forests (Niinemets & Anten, 2009; Aussenac, 2000; Poorter *et al.*, 2019; Lowman & Rinker, 1995) (Fig. 2).

In heterogeneous canopies [with high gap fractions], the distance from the outer canopy [to X?] is a better proxy for light environment than height (Parker 1995) and lower canopy light environments are highly variable, ranging from high light gaps to deeply shaded understory regions (Chazdon & Fetcher, 1984; Smith *et al.*, 2019; Tymen *et al.*, 2017)

Tropical forests with densely packed overstory trees limit light tosubsequent canopy layers and forest understories. Tropical forest floors receive approximately 1-2% of the incident light that hits the top of the canopy (Chazdon & Fetcher, 1984; Roberts *et al.*, 1990; Parker *et al.*, 2019), whereas mixed-wood boreal and Northern temperate forest floors receive around 4-5% of full sunlight (Bartemucci *et al.*, 2006). However, vertical canopy layers and forest floors also receive light permeating through canopy gaps and intermittent light penetration from crown, branch, and leaf movement caused by wind called sunflecks. Sunflecks can provide 10-80% of photon flux density for photosynthesis in canopy layers and understory depending on canopy attributes such as foliage density, height and architecture [Way and Pearcy 2012, REF]

This diffence in light regimes along a vertical profile is an important driver of plasticity in leaf traits, leaf physiology, adaptation, and thermal sensitivity. Leaves along a vertical intra-canopy gradient, as well as in inter-canopies, thus exhibit a variation in leaf trait adapaptions to a range of high light to shaded-ness (**???**; Doughty & Goulden, 2008; Fauset *et al.*, 2018; Michaletz *et al.*, 2016; Niinemets, 2006).

* Sunflecks: Leaky et al. 2003–from Marielle, “This is another, higher resolution axis of the variability of microenvironments that is probably quite important to address. (Also see the papers by Robin Chazdon on temporal variability of light environments). Maybe we will want to add these sentences (above) and something about sunflecks to a separate section that specifically addresses sources of variation in forest structure & microenvironments (e.g., vertical, horizontal, seasonal, diurnal, and with disturbance)?”

**Wind speeds are also higher at the top of the canopy (Fig. 2).** *(fill in some specifics from the NEON analysis)* Consistent with the results from NEON sites, higher wind speeds at greater heights within a forest canopy have been observed in both closed canopy forests (Barnard & Bauerle, 2016; McGregor *et al.*) and open savannas (Curtis *et al.*, 2019) in summer months [only in summer months?].

Wind speed in the upper canopy of a semi-deciduous tropical forest has been observed to be higher in the dry season than the wet season (Rey-Sánchez *et al.*, 2016) [*double check*]. Greater upper canopy wind speeds result in higher boundary layer conductance () for canopy leaves, which increases linearly with wind velocity (Daudet *et al.*, 1999). Large to heat transfer results in smaller difference in and . This is more typical of small leaves in the upper canopy that make them more efficient at dissipating heat than larger leaves (Bauerle & Bowden, 2011). In low wind conditions, because to heat transfer is small enough, in the upper canopy can become substantially more elevated than under high radiation (Martin *et al.*, 1999). Additionally, the thickness of the air layer is proportional to boundary layer resistance at the surface of the leaf through which water vapor diffuses after leaving the stomata (Roberts *et al.*, 1990; Martin *et al.*, 1999; Stokes *et al.*, 2006) this tends to be greater in the understory than canopy? [ref]

**Air temperature, , is sometimes significantly buffered by forest canopies (Fig. 2).** Studies comparing under forest canopies with nearby clearings have found lower maximum temperatures under forest canopies globally (De Frenne *et al.*, 2019), and recent evidence shows of a similar trend across Europe (von Arx *et al.*, 2012; Zellweger *et al.*, 2019) and in the northwestern United States (Davis *et al.*, 2019). Even though canopy cover buffers maximum air temperatures in the understory, inevitable increase in understory temperatures continue to be observed as a result of global increase in temperatures, however the buffering by canopy cover smoothens this warming in the understory (Bertrand *et al.*, 2020; Zellweger *et al.*, 2020b; Rollinson *et al.*)

Diurnal moderating capacity differs between forests with varying canopy structure, crown density, and seasons. Tropical, temperate broadleaved and non-pine conifer forests maintain lower daytime maximum temperatures than pine and boreal forests. Increase in crown density and leaf area index decreases light and higher maximum temperature permeability into forest understory, thus maintaining greater lower maximum daytime temperature. Comparitively open forests such as pine forests have sparse stands resulting in decreased buffering capacity in understory and closer air temperatures to nearby clearings (von Arx *et al.*, 2012; De Frenne *et al.*, 2019). This relationship is reveresed during the night, however, with pine forests maintaining warmer below canopy temperature than above(von Arx *et al.*, 2012)

Seasonally, maximum air temperatures were higher above than below tropical forest canopies during wet seasons in Panama (Rey-Sánchez *et al.*, 2016), temperate forests in Switzerland (von Arx *et al.*, 2012) and coastal Brazil (Fauset *et al.*, 2018, Tymen et al. 2017).Similarly, maximum temps were higher and humidity lower in gaps vs understory regions (both at 1.5 m above the ground, see Fig. 4 - again illustrating buffering effect of the canopy).However, similar maximum temperatures have been observed during the dry season of a semi-deciduous tropical forest in Panama partially because in the dry season some canopy trees were leafless, resulting in more light reaching the sub-canopy, and more air movement between subcanopy and above-canopy air(Rey-Sánchez *et al.*, 2016), similar results were observed in in a temperate deciduous forest in the eastern United States (McGregor *et al.*).

Minimum is also buffered by forest canopies under some conditions. Higher minimum temperatures under forest canopies relative to nearby clearings have been observed across Europe (Zellweger *et al.*, 2019) and in the northwestern United States (Davis *et al.*, 2019).(Martijn: should we refer to mechanisms at this point? (e.g., greater radiative heat loss in exposed areas resulting in lower Tmin)) However, similar minimum temperatures under forest canopies have been observed in tropical forests in Panama (Rey-Sánchez *et al.*, 2016) and coastal Brazil (Fauset *et al.*, 2018), as well as in a temperate deciduous forest in the eastern United States (Nakamura *et al.*, 2017; McGregor *et al.*).

*(Add something about risk of freeze.)*

**Humidity also varies across the forest vertical profile, being generally higher in the understory (Fig. 2).** - DETAILS - REFS - McGregor *et al.*

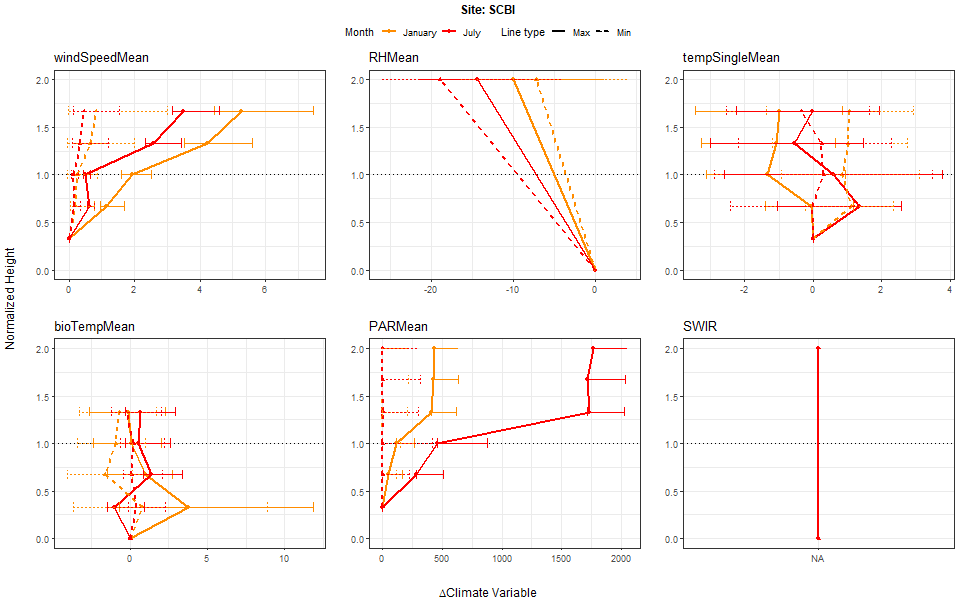
Along with temperature, forest canopies moderate relative humidity in below-canopy microclimates. In three European forest types (Broadleaved, Non-Pine Conifer, Pine) canopy buffering decreased daily maximum and increased daily minimum RH in below-canopy microclimate compared to a nearby open area. Moderating capacity was stronger under broadleaved and non-pine conifer forests than pine, and greater in wetter conditions, and in summer and autumn months than winter (von Arx *et al.*, 2012).

RH, in combination with temperature, determines vapor pressure deficit, . Atlantic forests during wet season tended to have higher , and in upper canopy and canopy gaps than lower in understory where and were lower (Fauset *et al.*, 2018; Tymen *et al.*, 2017).  
This means that canopy leaves tend to be exposed to higher *evaporative demand*, higher stomtal contrains and lower osmotic potential. (**???**). In North Eastern US temperate forests, upper canopy was observed to be more sensitive to , whereas understory was insensitive (Rollinson *et al.*, p. 2020)

**Finally, carbon dioxide (CO2) concentrations tend to be higher in the understory.** Higher in understory, particularly at dusk (Koike *et al.*, 2001). Higher in the understory overnight; difference persists during the day but is very small (Yang *et al.*, 1999). Differences in concentration are by far most pronounced near ground level, as well, concentrations of (CO2) mole fraction values have been observed to be higher in lower canopy leaves compared with upper canopy leaves (**???**)

Given that differences are small during the day when photosynthesis is active, and that even nighttime differences are modest at the height of understory tree crowns, CO2 concentration is unlikely to have much effect on the energy balance and metabolism of leaves across the forest vertical gradient.

If soil and stem respiration do not acclimate fully to rising temperatures, the greater amount of CO2 emitted at the forest floor could increase the vertical CO2 gradient in the future, but this would still only be a short-term effect in the early morning, as the CO2 would quickly diffuse through the canopy. Furthermore, increases in mortality of big trees (e.g. Senf et al. 2018) would increase canopy roughness and prevent build-up of CO2 concentration gradients.



**Figure 2. Vertical gradients in the biophysical environment, from NEON data.** Current placeholder figure is just one of several+ intended sites. See issue 2: <https://github.com/EcoClimLab/vertical-thermal-review/issues/2>.

**The strength of this buffering varies across forests, being influenced by both forest characteristics (Fig. 3) and the biophysical environment.** First, buffering increases with canopy cover and water availabity. \* greater cover –> lower max T and VPD, higher minT (Davis *et al.*, 2019) \* greater cover –> lower max T and light availability (Zellweger *et al.*, 2019) \* [Thom *et al.* (2020); Tymen et al. 2017 ; Jucker et al. 2018 ; Hardwick et al. 2015] The omega factor (McNaughton and Jarvis, 1983; Jarvis & McNaughton 1986) describes the degree of aerodynamic coupling between the vegetation and the atmospheric boundary layer; the lower the value of omega, the greater the coupling. "I wonder whether it would be useful to introduce such ‘formal’ terms used to describe what is essentially the same as buffering effect of canopies. I’d have to read up some more to see if there are papers showing what sort of canopy characteristics influence omega.

[https://doi.org/10.1016/S0065-2504(08)60119-1"-M.Slot](https://doi.org/10.1016/S0065-2504(08)60119-1%22-M.Slot)

*Presumably, buffering would also be affected by canopy roughness, which affects turbulent air flow and the canopy boundary layer.* Taller trees don’t necessarily increase buffering (Zellweger *et al.*, 2019). “They found that taller forests (which coincided with forests of higher LAI) had lower mean and max values of VPD and temperature” [Jucker, T., Hardwick, S.R., Both, S., Elias, D.M., Ewers, R.M., Milodowski, D.T., Swinfield, T. and Coomes, D.A., 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Global change biology, 24(11), pp.5243-5258] .See Jucker et al. 2018 - max height was highly correlated to both LAI and surface roughness

Species that have higher shade casting ability such as braodleaved trees increase T buffering (Zellweger *et al.*, 2019, p. @vonarxSpatiotemporalEffectsForest2012) The strength of buffering also varies with respect to geographic and climatic factors. \* Distance to coast, topographic position, elevation (Zellweger *et al.*, 2019) \* (Davis *et al.*, 2019)–Proximity to riparian areas tends to sustain buffering, protecting understory temperatures even during increasing temperatures (Davis *et al.*, 2019) However vertical climate gradients within forests are known to be steeper than those driven by elevation and latitude (Nakamura *et al.*, 2017; Martin *et al.*, 2020)



**Figure 3. Role of canopy permeability in shaping temperature buffering, from NEON data.** Current placeholder figure is Nidhi’s first rough analysis. See issue 2: <https://github.com/EcoClimLab/vertical-thermal-review/issues/2>.

## Trait variation

Leaf traits are shaped on the basis of light and height and show different degrees of foliar plasticity in accordance with the intensity and availability of light which also optimizes water uptake, heat and C uptake by leaves across forest vertical strata. After the formation of leaves to integrated light, it takes 30-60 days for traits to stabalize in woody and herbaceous species (Niinemets, 2016). A network of sensory photoreceptors in leaves such as phytochromes among others mediate response to PAR, and ratio of red to far red radiation [R:FR] falling on the surface. This enables acclimation or avoidance response through development of necessary traits [Casal, 2013]. As a result, degrees of high irradiance gives rise to variations of sun-leaf traits compared to degrees of low irradiance– characterized by shade– shapes variations of shade-leaf traits [Poorter *et al.* (2019); Sack et al 2006], which ultimately also shapes leaf structural, chemical and physiological traits as well [Keenan and Niinemets et al. 2016].

Increasing number of studies point towards the importance for incorporating sun and shade in modelling leaf economic spectrum (LES) within-canopy gradient(Chen *et al.*, 2020) because LES was ‘built’ using mainly sun (upper canopy) leaves; given the vastly different light environments at the bottom of the canopy (and that most leaves in the canopy are likely to be shade leaves) there is a strong research need to better characterise trait relationships and leaf responses through the whole vertical canopy [Keenan and Niinemets 2016]. However, there is also concern for ambiguity in simplified cateogorization of ‘sun’ and ‘shade’ leaves due to variation based on light within-canopy, across functional groups, in canopy gaps, height and ontogeny (Niinemets *et al.*, 2015; Ishii *et al.*, 2018) as well as geographically (Ishii *et al.*, 2018). Classification for sun and shade tolerance rankings have been highlighted by multiple studies [Baker 1949; Niinemets (2006); Feng et al. 2018] such as from Niinemets (2006) are as follows: “The five-level scale used for shade tolerance (1,very intolerant; 2, intolerant; 3, moderately tolerant; 4,tolerant; 5, very tolerant) corresponds approximately to the following light availabilities expressed as percentage of full sunlight: 1,>50%; 2, 25-50%; 3, 10-25%; 4, 5-10%; 5, 2-5%”. “Additionally, shade leaves in the understory are of three categories; 1. shade leaves of canopy trees–top of the tree is sun exposed, bottom is shaded. 2. seedlings/saplings of canopy trees that will eventually, if they survive, reach the canopy. 3 understory plants that complete their lifecycle in the shaded understory. These groups are likely to have different traits, and if we expect’shade’ plants to have a different sensitivity to climate change than sun leaves, the consequences of climate change for demography and species community composition of the forest will depend strongly on the category of shade plants being considered”.[refs, -Martijn Slot]

**Inter-species vertical gradient leaf trait variation**

Taller trees in dense forests tend to be exposed to greater irradiance than lower canopy and shorter understory trees shaded by overstory. As a result, sun and shade leaf trait dichotomy has been established across species by various studies where typical sun leaves are often smaller in size and width, thicker, hairier, with thicker cuticle and more lobated than shade leaves [Rozendaal et al. 2006, Mathur et al. 2018, more REFS].

However, the combination of stressors taller trees’ foliage experience are different from the combination of stressors understory shorter trees’s foliage experience. For example, overstory sun leaves experience greater loads of PAR, , elevated temperatures, wind speed, etc. whereas for understory–shade or limitation of light, niche competition, herbivory etc. These pressures also contribute to the development of necessary traits that is primarily mediated by light response. Overstory sun leaves are subjected to overheating pressures, thus through developed traits of increased stomatal density, transpiration and water supply along with increased convective heatloss by reducing boundary layer resistance, sun leaves are able to maintain optimum temperature. Additionally, overstory sun leaves tend to have long-lived leaves with high LMA while shade leaves of canopy trees have large leaves with low LMA. Adaptive traits in understory enable light capture efficiency while maintaing larger width leaves with comparitevely fewer stomtal density as a result of available water, lesser , and wind speed. “Spending their lifecycle in the shade means they have different pressures than plants that get the bulk of their carbon from sun-exposed leaves, but can maintain a few layers of shade leaves as well.”[-Martijn].Those differences in traits are likely to affect their thermal properties as well.Leaves act as windows to plant performance enhacing plant adaptation to changing environment, thus traits acclimated to prior stressors have been suggested to enable whole plant to respond differently to forcoming stress (Rozendaal et al. 2006; Niinemets, 2010)

However, even with distinct features of sun and shade traits, trait adaptation to light is done in such a way where light use efficiency for photosynthesis is maximized at both high or low light, while also adapting to other stressors as mentioned above. In light limited conditions, shade leaves increase light capture efficiency through increasing their specific leaf area [SLA] and by investing in chlorophyll at a mass basis–“leads to a similar chlorphyll content on an area basis compared with sun leaves. This makes shade leaves realize a similar light capture to sun leaves at a lower biomass investment” [Chazdon et al. 1996, Poorter et al. 2000, Rozendaal et al. 2006]

With increasing height and age, competion for light decreases as availibity of light increases in dense forests. However, depending on growth strategies of species occupying the understory, leaf traits might differ due to species inherent light requirements. Early successional species are considered more shade intolerant than late successional species that are more shade tolerant. Ontogenic differences between the two in the understory suggests lower leaf dry mass per area () in shade tolerators than in intolerators, greater photosynthetic capacity in low light and greater carbon gain capacities[Niinemets, 2006].Rozendaal et al. 2006, Koike et al. 2001 has more info about this.

**Intra-canopy on the same species leaf trait variation**

Several studies point towards common variations and differences in leaf trait plasticity within-species and at an intra-canopy gradient which shapes leaf structural and biochemical traits (**???**; Sack *et al.*, 2006; Niinemets *et al.*, 2015). The differences among these traits contribute to leaf heat dissapation strategies and leaf temperature across the gradient (Fauset *et al.*, 2018; Michaletz *et al.*, 2016) Table 1. summaries relevant traits for thermal sensitivity.

[I think that this distinction should be addressed throughout the manuscript, so that it is always clear that the reader knows whether the cited references are about inter- or intra-specific variation, and that we address the different trait axes (Marielle made a comment on this earlier as well, that within species patterns may not follow leaf economics spectrum expectations). Ideally we would address the different categories, but if lack of information forces us to focus on just within species or just across species, this should still be made clear. photosynthesis, and canopy-level carbon uptake. They don’t have to be treated separately, but it should always be clear which is being referred to. And in the consequences for scaling section this is of course also relevant.] [Add something about how leaf traits along the vertical canopy profile are different than the expectation from leaf economic spectrum (LES)? Chen et al. 2020 is a good paper to help frame this . They make an important point in that paper that we may also want to make here: that the LES was ‘built’ using mainly sun (upper canopy) leaves; given the vastly different light environments at the bottom of the canopy (and that most leaves in the canopy are likely to be shade leaves) there is a strong research need to better characterise trait relationships and leaf responses through the whole vertical canopy - hence the importance of this review. Keenan & Niinemets 2016 will also be helpful in making this point.]–M N. Smith

**Many traits vary with height and/or between sun and shade leaves on the same species (Table 1).** Here, we focus on intra-canopy traits that are important for shaping leaf temperature () and thermal sensitivity.



(*For latest version of table, see tables.pdf.*)

Are traits shaped more by height or light? Height is more important than light in determining leaf morphology in a tropical forests (Cavaleri et al. 2010) - (Cavaleri et al. 2008) - from Martijn: “If I remember correctly, height and light exposure are closely correlated and things like LMA scale with both, but above a certain level of light exposure, the effect of additional light disappears, while the relationship of the morphological traits with height continues. I have often been a bit skeptical about assuming height drives morphology, as most of the work that convincingly shows that (and relates it to turgor pressure for example) is from 100 m tall redwoods.” -“Our study suggests that height plays an important role in the leaf traits, in contrast with previous findings (Baranski, 1975; Sack et al., 2006).In Quercus. alba and Quercus. velutina, loba-tion decreased with increasing tree height. Lobation allows air passage and light penetration in the tree canopy (Sack et al., 2006; Semchenko & Zobel, 2007)” (Kusi & Karsai, 2020)

*Leaf area / characteristic dimension*: - Recent paper on influence on leaf size/shape in PCE – certain aspects of leaf shape were not as relevant as expected (Leigh et al. 2017? <https://onlinelibrary.wiley.com/doi/full/10.1111/pce.12857>) - Max stomatal conductance - increases with canopy height (Kenzo et al. 2015) Max transpiration rate - increases with canopy height (Kenzo et al. 2015). Leaf width and characteristic dimension influence boundary layer resistance which generally is greater in wider understory leaves than upper canopy. Leaf temperature increases with leaf area {Wright et al. 2019} -Boundary layer resistance and thermal sensitivity also depends of leaf width, leaf size and structure. Increase in leaf width increases stomatal resistance– dependent on stomtal activity and boundary layer resistance (Fauset *et al.*, 2018). Leaf characteristics such as lobes, leaf elongation and serration, all facilitate in dissapating heat more efficiently. Leaf lobes are deeper in exposed canopy than in shaded understory, as well as leaf elongation and serration are more pronounced in sun exposed canopies[Vogel 1970; Roth-Nebelsick 2001; Schuepp 1993; Sack et al. 2006]. -Boundary layer thickness, depth and boundary layer resistance increases with leaf size and effective leaf width [along the vertical gradient], such that the rate of heat convection per unit area between leaf and air is lower for large leaves and greater for small leaves, therefore allowing small leaves to dissapate heat more efficiently than large leaves (Leigh *et al.*, 2017).

*Thermal time constant (probably not a lot out there)* - Curtis et. al, 2018 – higher in more exposed leaves (heat up slower, cool slower) - Michaeletz has used this in theoretical calculations (Michaeletz et al. 2016 and 2015? I have Michaletz’s code to calculate the thermal time constant, so if there are data, or general tendencies for changes in leaf area, LMA, leaf width and leaf dry matter content we can determine how these trends would translate into changes in thermal time constant. In practice, an important driver seems to be leaf water content per unit area (I think Lawren might have mentioned this as well in our meeting), so if we can conclude that that is something that scales with the vertical gradient, then we can make an informed guess about how the thermal time constant will change–Martijn Slot -Effective leaf width defined as the largest circle that can be inscribed in a leaf is an effective predictor of leaf thermal time constant and leaf boundary layer thickness. Large leaves have greater effective leaf width which increases their thermal time constant by prolonging leaf cooling time compared to small leaves that have a smaller effective leaf width, and thus small thermal time constant with shorter cooling time. Increased leaf width typical in larger leaves was also observed to increase leaf to air temperature difference. (Leigh *et al.*, 2017)

*Carotinoids/Xanthophyll cycle pigments* - photoprotective- disseminate heat, acclimate to high T. THese are proportional to irradiance - antioxidant scavenging function- protect against cellular damage - Koniger et. al. 1995, and Matsubara et al. 2009

*Isoprene production* - Isoprene production *capability* as a trait (actual isoprene production is in section 4. I’m not sure whether Ty’s content belongs here or in that section)

*(Paragraph on intra- vs inter-specific variation)*

* *Are patterns (in traits, metabolism, ecology) driven by tree height or exposure?*

## Leaf temperature and hydraulics

**Many of the biophysical and trait variable reviewed above affect leaf temperature, , which in turn has a strong influence on leaf metabolism (see following section).** is determined by the energy balance of a leaf and can be estimated based on basic biophysical principles (Campbell & Norman, 1998; Muir, 2019) (Fig. 3). - As light availability typically increases with tree height, leaf temperature which is largely of function of radiation input, does as well (Michaletz *et al.*, 2015). Direct sunlight in upper canopy leaves increases leaf temperature, [sometimes 1-7C above ambient air temperature, making upper canopy leaves susceptible to heat stress] more than scattered light in lower shaded leaves (Mau *et al.*, 2018b) While small leaves remain within a few degrees of , regardless of stomatal conductance, wider leaves can have temperatures deviating more from air temperature.(Fauset *et al.*, 2018) Large leaves can be significantly cooler than under low radiation with stomata open, and significantly hotter under high radiation with stomata closed.  
Leaves with open stomata and high radiation loads maintain similar to , with coolest leaves at intermediate sizes (~10mm). Shaded understory leaves should tend to maintain cooler daytime leaf temperatures for any given level of stomatal conductance. However, counteracting this, lower wind speed in understory would reduce latent heat loss. Thus, under hot conditions, canopy leaves exposed to higher wind speeds would be most effective at cooling when sufficient water is available to maintain high stomatal conductance; however, their can be highly elevated above when stomatal conductance is limiting. - increase in air temperature, increases VPD, decrease in stomtal conductance during miday leading to decrease in CO2 in leaf = increase in leaf temperature in upper canopy. (Fauset *et al.*, 2018)



**Figure 3. Leaf temperature in response to (a) XXX, (b) XXX (key trait or environmental variables).** Examples to be produced based on energy balance model using the tealeaves R package of Muir (2019): <https://github.com/EcoClimLab/vertical-thermal-review/issues/6>. Current placeholder shows figures from Campbell&Norman.

**Aligning with biophysical expectations, field observations have shown that leaf temperatures are influenced by the biophysical environment and leaf traits.** 1. Air T 2. Solar radiation 3. Leaf traits - Michaletz et al have done some interesting work on leaf thermoregulation in relation to various leaf traits. I don’t think there is sun vs shade tests, but we could look at how this might translate, or how some of the traits he has calculated might differ between sun and shade leaves. For example, he has this thermal time constant parameter that is calculated from leaf mass per area, leaf dry matter content, and some environmental parameters. E.g.: DOI: 10.1038/nplants.2016.129, <http://dx.doi.org/10.1016/j.tree.2015.09.006>

**When vertical gradients in the biophysical environment and leaf traits combine to shape leaf energy budgets, under some conditions tracks and therefore differs little between understory and canopy (Fig.** 2?**).** In a broadleaf deciduous forest, nighttime ’s were similar in the canopy and understory (Bolstad et al. 1999). Similarly, during the dry season in a tropical moist forest in Panama… (Rey-Sánchez et al. 2016). **However, canopy leaves can reach much higher maximum , and higher , than understory leaves.** -Large leaf to air temperature differences and high leaf temperatures were found in upper canopy of Atlantic, Brazil Forests despite much lower air temperature due to high solar radiation loads. However, leaf temperatures themselves were moderaed by air temperature. (Fauset *et al.*, 2018). - (Slot et al. 2019) and refs therein - (Fauset et al. 2018) Sun leaves can also be cooled relative to more than shade leaves (Rey-Sánchez et al. 2016). There’s some hint of this in Bolstad et al. 1999.

*(Because hydraulics are key to leaf T, we should include some of that here–e.g., water on leaves and leaf water content)*

## Leaf metabolism and thermal responses

Leaf metabolism is strongly shaped by leaf temperature, and by the traits and environmental drivers reviewed above, all of which vary across vertical forest gradients (Fig. 1). However, as we detail below, there are limited studies comparing thermal responses of sun and shade leaves (Table 2).



(*For latest version of table, see tables.pdf.*)

*Stomatal conductance* Photosynthesis can be largely constrained by stomatal conductance. -“Sun exposed outer canopy leaves in tropical trees can experience temperatures up 48 C during diurnal cycle, midday stomtal closure reduces transpitrational cooling” thus elevating leaf temperature greater than air temperature (Slot et al. 2019)

*Photosynthesis*

**Photosynthesis is generally higher in sun leaves– a fact that is well-established (Niinemets 2007 ; Kenzo et al. 2015 ; Slot et al. 2019; Chen et al. 2020) and observed in numerous field studies.** This is primarily driven by the greater light available to sun leaves. In response to the greater light availability, sun leaves have traits allowing greater photosynthetic rates at high light, including higher concentration of Rubsico, multiple layers of palisade parenchyma, and saturation level differs between leaves and canopies, with leaves saturating at lower light level than canopies (while a certain amount of light saturates the photosynthetic capacity of the leaf, increasing the amount of light in the canopy may increase photosynthesis in the shaded part of the canopy) The vertical gradient in photosythetic rates is also influenced by available concentration of N and P. .[thoughts: plasticity vs change in tree species composition through the canopy; differences in variability of microenvironments through the profile - highest lower down in canopy?; life history / investment strategies and hence, leaf life spans at leaves at the top vs bottom of the canopy]– M N. Smith [agreed. Again the importance of differentiating between within-species and among species trait variation. Also; steepness of the vertical gradient in light and VPD. In very tall trees a gradient in water potential might cause a gradient in stomatal limitations of net photosynthesis]

Photosynthesis increases with increasing irradiance, and saturates at quatum flux density of 400 to 700nm . Photosynthesis has a peaked response to temperature, where photosynthesis is commonly found to be maximized at the prevalent ambient growing season conditions (Tan et al. 2017; Slot & Winter 2017).Beyond the optimum photosynthesis decreases as a result of stomatal closure (e.g. Slot & Winter 2017; Smith et al. 2020 [temperate/boreal refs needed) and eventually due to biochemical constraints (refs. e.g. Sage & Kubien 2007; Varhammer et al. 2015 ).Photosynthesis will also be affected by heat stress, when photoinhibition reduces photosynthesis either as a result of photoprotective; non-photochemical quenching or related to irreversible leaf damage leading to leaf necrosis. Leaves in upper canopy tend to experience more heat stress and greater photoinhibition than lower canopy leaves in conditions of water stress or drought. (Niinemets *et al.*, 2015)

**While sun and shade leaves differ dramatically in , the temperature sensitivity of photosynthesis does not appear to differ substantially between sun and shade leaves** Biophysically, we might expect that sun leaves should tend to have a stronger temperature-dependence and higher temperature optima than shade leaves (Fig. 14.5; *revisit this!*) (Campbell and Norman 1998) as observed by earlier studies, suggesting that the interaction between light gradient and temperature response along vertical canopy profile implied there to be a spectrum of temperature responses of , and along the gradient [Niinemets *et al.* (2004); Harley and Baldocchi 1995, Friend, 2001]. However, this does not appear to be the case based on the limited number of field studies that have compared temperature sensitivity of photosnythesis in sun and shade leaves. For 3 species in Panama, Hernández *et al.* (2020) and (**???**) found that the optimum temperature for sun leaves tended to be slightly higher than that of shade leaves, but differences were not significant. Similiar results were found for and (**???**, Hernandez et al.2020) Mau et al. found no trend in the optimum temperature for net photosynthesis along a height gradient in Puerto Rico, and no significant trend in temperate trees (Mau *et al.*, 2018a).

**Leaf thermal tolerance (Tcrit/ T50)** - define. Typical values ~45-50C, varying somewhat across latitude/climate (O’sullivan et al. 2017), with elevation [Feeley *et al.* (2020); Slot unpublished data], with leaf traits (Sastry et al. 2018, Zhang *et al.*, 2012).

**Thermal tolerance (e.g., ) varies with exposure, but there are no studies isolating effect of height.** For two of three species studied in a tropical moist forest in Panama, was slightly lower for shade than sun-exposed leaves, both measured near ground level (Slot et al. 2019). Similarly, for *Acacia Papyrocarpa* (Benth.) trees in an arid region of southern Australia, higher was observed in more exposed (North-facing) canopy positions (Curtis et al. 2019). We’re not aware of any other studies on this.“we may want to argue that we have no a priori reasons to expect thermal tolerance to scale with height per se (or do we?). I think it makes sense to expect variation with light exposure because of the associated differences in temperature you can expect the leaves to be exposed to, but height itself should not affect heat tolerance other than through associated traits perhaps”–Martijn Slot

*Respiration*

**Similar to photosynthesis, respiration tends to be higher in sun leaves (Chen et al. 2020), but its temperature sensitivity appears to be similar between between sun and shade leaves.** At increasing temperatures, Photosynthetic System 2 [PS2] is particularly vulnerable. Damage to pS2 can lead to decreased electron transport rates and photosynthetic failure. Irreversible damage to PS2 is done at 40-60C (Baker 2008; Feeley *et al.*, 2020) (Bolstad et al. 1999) did a study at Coweeta, including elev gradient. Found higher respiration (at reference T) in canopy leaves (Bolstad *et al.* (1999)). (*Martijn has some unpublished data on this that we might include:* [*https://github.com/EcoClimLab/vertical-thermal-review/issues/8*](https://github.com/EcoClimLab/vertical-thermal-review/issues/8)*.*) At Coweeta, Q10 showed a variable pattern, with a slight tendency to increase down the canopy (Bolstad *et al.*, 1999). (*Martijn has some unpublished data on this that we might include.unpublished data showing higher Q10 in shade than in sun leaves for 10 species or so. May make sense to include here:* [*https://github.com/EcoClimLab/vertical-thermal-review/issues/8*](https://github.com/EcoClimLab/vertical-thermal-review/issues/8)*.*) Combining reference respiration and , Bolstad *et al.* (1999) found a modest net decrease in R for understory leaves relative to canopy leaves as T increases (*see their Fig. 1*).“Higher values in the functional groups of upper canopy where temperatures are the highest may lead to exponential loses of C with increasing global temperatures depending upon the ability of canopy leaves to acclimate” (Cavaleri *et al.*, 2008) Thus, Bolstad *et al.* (1999) found evidence of acclimation, but there remained a declining trend of respiration with elevation.

*VOC production*

**Isoprene production** - high emission rates occur in the mid-canopy, and even from very small statured trees and shrubs, at a site in the Brazilian Amazon (Taylor et al., in prep). - The high temperature carbon compensation point of sun leaves is higher in isoprene emitting species than in non-emitting species, so it is to be expected that other aspects of heat tolerance will be similarly affected by isoprenes (<https://doi.org/10.1111/pce.13564>). - Within species, isporene production scales with light/ T

## Ecosystem Scaling & implications

### Distribution of species and traits across the vertical profile

\*(This section should address inter-specific vs intra-specific variation, as Tables 1 and 2 refer to intra-specific variation, but most models will focus on trait variation across strata, regardless of species).

**Differences across forest vertical gradients in biophysical conditions, plant traits, and metabolism and its thermal responses scale up to affect whole-tree ecology in several ways.** First, vertical gradients in the biophysical environment shape which plant strategies, or sets of traits, are competitive in understory versus canopy conditions. - *Spring and fall leaf phenology in temperate deciduous forests (Augsburger). Mechanism: more moderate conditions (T, wind) in understory (REF).* *Among species that can be deciduous, greater proportion of deciduous individuals in larger size classes (Condit et al. 2000). One potential mechanism is lower temperature/hydraulic stress in understory* - something on isoprene production?

**Appears to affect community change under warming (Zellweger et al. 2020).**

### Scaling to tree level: demography

**Vertical gradients also affect tree growth and survival, and how these respond to climatic variation.** There are numerous demographic differences between understory and canopy trees, which have been linked to both the physical environment and plant traits (e.g., REFS), and we will not attempt to review those here. More interesting in this context is how these shape differences in the climatic sensitivity of growth and mortality. Many observations of larger trees suffering more during drought (Bennett et al. 2015). One likely mechanism behind this pattern is that the crowns of larger trees exist higher in the vertical profile and therefore are exposed to higher evaporative demand and solar radiation (McGregor *et al.*). Although drought is primarily a hydraulic problem, lack of water –> lower gs –> higher leaf T, so leaves face tradeoffs of water loss vs potentially damaging leafT.

**There is also recently emerging evidence that understory trees tend to exhibit greater growth declines with under mesic conditions.** In eight forests across the northeast United States, growth rates of understory trees declined sharply at higher (Rollinson et al., in review). Similarly, our previously unpublished analysis shows that in a broadleaf deciduous forest in Virginia, understory trees in a Mid-Atlantic forest responded more negatively to warmer than did canopy trees (Fig. **4**; Appendix S4). This pattern is initially counter-intuitive in that sun-exposed leaves can experience greater elevation of over than shade leaves (Fig. **3?**). However, given adequate moisture to sustain high , canopy leaves exposed to more wind and lower humidity should be more effective at cooling when exceeds physiological optima (Fig. **3**). It is also possible that competition is accelerated under warmer temperatures.

Additionally, increased exposure to light increases non structural carbon reserve (NSC), plant height, foliage robustness, while also increasing evapotranspiration, decreasing hydraulic conductivity, increasing chances of photoinhibition in leaves should water availbility become limited, however with available water overall sensitivity to stress decreases. Understory shaded/younger trees have comparitively less NSC reserve due to light limitation as a primary stressor [which differs among shade-tolerant/intolerant], decreased plant biomass, increased leaf biomass, and decreased evapotransition demands, as well as greater investment in light harvesting than in photosynthesis–with greater overall sensitivity to stress and reduced tolerance. Larger NSC reserves in trees with greater light and water availability allows them to tolerate greater number of stressors compared to understory/younger trees that are able to tolerate only a fewer stressors making them overall more sensitive to stress [such as temperature]. Thus, overall stress sensitivity decreases and tolerance increases with increasing height, light and age.(Niinemets, 2010)

Interaction between degrees of shade x ontogeny x height with rising temperature needs more scietific attention because a huge part of understory vegetation lies within variations of light and shade spatio-temporal gradient.



**Figure 4. Temperature sensitivity of tree growth (derived from tree rings) for understory versus canopy trees.** THIS IS A ROUGH PLACEHOLDER– KAT WILL PLAY WITH POTENTIAL VERSIONS. IF OUR IN-PREP TREE RING ANALYSIS METHODS PAPER IS ACCEPTED AHEAD OF THIS, WE CAN HIGHLIGHT RESULTS FROM THAT, WHICH ARE MORE RELIABLE. Analysis methods described in Appendix S4. OUTLIER HERE IS SHADE-TOLERANT BEECH. Data from Helcoski et al. 2019.

## Implications for Modeling / Scaling / Future Climate Projections

Elsa–The content below could probably be integrated in the above [Ecosystem Scale Implications] section, with subsections focusing on: - Suggested implications at the ecosystem scale based on literature - How do models currently integrate or not integrate these concepts and dynamics - What major gaps in knowledge and/or important questions emerge from this review (i.e. a lot of focus on droughts justifiably, but understanding heterogeneous impacts of temperature increases on forest ecosystems, particularly at vertically resolved scales is also important.) - What does that mean for about ability to predict/understand how forest ecosystems will respond in the future?

E.g. see de Pury & Farquhar, 1997 : though likely an improvement over ‘big-leaf’ models, models that separate the canopy into sunlit and shaded portions (sun/shade models) may not be able to capture important within-canopy variation in terms of leaf dynamics (e.g. seasonal shifts in vertical leaf area distributions, Smith et al. 2019) and functions (e.g. thermal responses, as we present in this paper). Hence, multi-layered ecosystem models may be necessary for accurately projecting future forest function.

(Nakamura *et al.*, 2017)–> modelling ideas?

*(do we need a section on ecosystem function– e.g., transpiration, gpp?)*

### Implications for climate change responses

* CO2 may lead to denser understory (Martijn)
* Influence of increasing temperatures on species compositions and feedbacks to future forest microclimates and function?

–Variation across horizontal biophysical gradients (climate, soils, etc.)(E.O)

## Conclusions

## SI files

Appendix S1. Methods for NEON vertical profiles

Appendix S2. Methods for leaf energy balance modeling

Appendix S3. Methods for literature review

Appendix S4. Methods for SCBI tree-ring analysis

## References

Allen CD**,** Breshears DD**,** McDowell NG. **2015**. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: art129.

Almeida DRA de**,** Nelson BW**,** Schietti J**,** Gorgens EB**,** Resende AF**,** Stark SC**,** Valbuena R. **2016**. Contrasting fire damage and fire susceptibility between seasonally flooded forest and upland forest in the Central Amazon using portable profiling LiDAR. *Remote Sensing of Environment* **184**: 153–160.

Aussenac G. **2000**. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* **57**: 287–301.

Barnard DM**,** Bauerle WL. **2016**. Seasonal Variation in Canopy Aerodynamics and the Sensitivity of Transpiration Estimates to Wind Velocity in Broadleaved Deciduous Species. *Journal of Hydrometeorology* **17**: 3029–3043.

Bartemucci P**,** Messier C**,** Canham CD. **2006**. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Can. J. For. Res.* **36**: 2065–2079.

Bartholomew DC**,** Bittencourt PRL**,** Costa ACL da**,** Banin LF**,** Costa P de B**,** Coughlin SI**,** Domingues TF**,** Ferreira LV**,** Giles A**,** Mencuccini M ***et al.*** **2020**. Small tropical forest trees have a greater capacity to adjust carbon metabolism to long-term drought than large canopy trees. *Plant, Cell & Environment* **43**: 2380–2393.

Bauerle WL**,** Bowden JD. **2011**. Separating foliar physiology from morphology reveals the relative roles of vertically structured transpiration factors within red maple crowns and limitations of larger scale models. *Journal of Experimental Botany* **62**: 4295–4307.

Bennett AC**,** McDowell NG**,** Allen CD**,** Anderson-Teixeira KJ. **2015**. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**: 15139.

Bertrand R**,** Aubret F**,** Grenouillet G**,** Ribéron A**,** Blanchet S. **2020**. Comment on ‘Forest microclimate dynamics drive plant responses to warming’. *Science* **370**.

Bertrand R**,** Lenoir J**,** Piedallu C**,** Riofrío-Dillon G**,** de Ruffray P**,** Vidal C**,** Pierrat J-C**,** Gégout J-C. **2011**. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**: 517–520.

Bolstad PV**,** Mitchell K**,** Vose JM. **1999**. Foliar temperature–respiration response functions for broad-leaved tree species in the southern Appalachians. *Tree Physiology* **19**: 871–878.

Bonan GB. **2016**. *Ecological climatology: Concepts and applications*. New York, NY, USA: Cambridge University Press.

Campbell G**,** Norman J. **1998**. *An Introduction to Environmental Biophysics*. New York: Springer.

Cavaleri MA**,** Oberbauer SF**,** Ryan MG. **2008**. Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell & Environment* **31**: 473–483.

Chazdon RL**,** Fetcher N. **1984**. Photosynthetic Light Environments in a Lowland Tropical Rain Forest in Costa Rica. *Journal of Ecology* **72**: 553–564.

Chen X**,** Sun J**,** Wang M**,** Lyu M**,** Niklas KJ**,** Michaletz ST**,** Zhong Q**,** Cheng D. **2020**. The Leaf Economics Spectrum Constrains Phenotypic Plasticity Across a Light Gradient. *Front. Plant Sci.* **11**.

Curtis EM**,** Knight CA**,** Leigh A. **2019**. Intracanopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of a desert tree (Acacia papyrocarpa). *Oecologia* **189**: 37–46.

Daudet FA**,** Le Roux X**,** Sinoquet H**,** Adam B. **1999**. Wind speed and leaf boundary layer conductance variation within tree crown: Consequences on leaf-to-atmosphere coupling and tree functions. *Agricultural and Forest Meteorology* **97**: 171–185.

Davis KT**,** Dobrowski SZ**,** Holden ZA**,** Higuera PE**,** Abatzoglou JT. **2019**. Microclimatic buffering in forests of the future: The role of local water balance. *Ecography* **42**: 1–11.

De Frenne P**,** Rodríguez-Sánchez F**,** Coomes DA**,** Baeten L**,** Verstraeten G**,** Vellend M**,** Bernhardt-Römermann M**,** Brown CD**,** Brunet J**,** Cornelis J ***et al.*** **2013**. Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci U S A* **110**: 18561–18565.

De Frenne P**,** Zellweger F**,** Rodríguez-Sánchez F**,** Scheffers BR**,** Hylander K**,** Luoto M**,** Vellend M**,** Verheyen K**,** Lenoir J. **2019**. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* **3**: 744–749.

Doughty CE**,** Goulden ML. **2008**. Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences* **113**.

Fauset S**,** Freitas HC**,** Galbraith DR**,** Sullivan MJP**,** Aidar MPM**,** Joly CA**,** Phillips OL**,** Vieira SA**,** Gloor MU. **2018**. Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment* **41**: 1618–1631.

Feeley K**,** Martinez-Villa J**,** Perez T**,** Silva Duque A**,** Triviño Gonzalez D**,** Duque A. **2020**. The Thermal Tolerances, Distributions, and Performances of Tropical Montane Tree Species. *Frontiers in Forests and Global Change* **3**.

Harley P**,** Guenther A**,** Zimmerman P. **1996**. Effects of light, temperature and canopy position on net photosynthesis and isoprene emission from sweetgum (Liquidambar styraciflua) leaves. *Tree Physiol* **16**: 25–32.

Hernández GG**,** Winter K**,** Slot M. **2020**. Similar temperature dependence of photosynthetic parameters in sun and shade leaves of three tropical tree species. *Tree Physiol* **40**: 637–651.

Huang M**,** Piao S**,** Ciais P**,** Peñuelas J**,** Wang X**,** Keenan TF**,** Peng S**,** Berry JA**,** Wang K**,** Mao J ***et al.*** **2019**. Air temperature optima of vegetation productivity across global biomes. *Nature Ecology & Evolution* **3**: 772–779.

Ishii HR**,** Horikawa S-i**,** Noguchi Y**,** Azuma W. **2018**. Variation of intra-crown leaf plasticity of Fagus crenata across its geographical range in Japan. *Forest Ecology and Management* **429**: 437–448.

Kafuti C**,** Bourland N**,** De Mil T**,** Meeus S**,** Rousseau M**,** Toirambe B**,** Bolaluembe P-C**,** Ndjele L**,** Beeckman H. **2020**. Foliar and Wood Traits Covary along a Vertical Gradient within the Crown of Long-Lived Light-Demanding Species of the Congo Basin Semi-Deciduous Forest. *Forests* **11**: 35.

Koike T**,** Kitao M**,** Maruyama Y**,** Mori S**,** Lei TT. **2001**. Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology* **21**: 951–958.

Kusi J**,** Karsai I. **2020**. Plastic leaf morphology in three species of Quercus: The more exposed leaves are smaller, more lobated and denser. *Plant Species Biology* **35**: 24–37.

Leigh A**,** Sevanto S**,** Close JD**,** Nicotra AB. **2017**. The influence of leaf size and shape on leaf thermal dynamics: Does theory hold up under natural conditions? *Plant, Cell & Environment* **40**: 237–248.

Lowman M**,** Rinker HB. **1995**. Forest Canopies. In: Endeavour.

Martin RE**,** Asner GP**,** Bentley LP**,** Shenkin A**,** Salinas N**,** Huaypar KQ**,** Pillco MM**,** Ccori Álvarez FD**,** Enquist BJ**,** Diaz S ***et al.*** **2020**. Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Front. Plant Sci.* **10**: 1810.

Martin TA**,** Hinckley TM**,** Meinzer FC**,** Sprugel DG. **1999**. Boundary layer conductance, leaf temperature and transpiration of Abies amabilis branches. *Tree Physiology* **19**: 435–443.

Mau A**,** Reed S**,** Wood T**,** Cavaleri M. **2018a**. Temperate and Tropical Forest Canopies are Already Functioning beyond Their Thermal Thresholds for Photosynthesis. *Forests* **9**: 47.

Mau A**,** Reed S**,** Wood T**,** Cavaleri M. **2018b**. Temperate and Tropical Forest Canopies are Already Functioning beyond Their Thermal Thresholds for Photosynthesis. *Forests* **9**: 47.

McDowell NG**,** Allen CD**,** Anderson-Teixeira K**,** Aukema BH**,** Bond-Lamberty B**,** Chini L**,** Clark JS**,** Dietze M**,** Grossiord C**,** Hanbury-Brown A ***et al.*** **2020**. Pervasive shifts in forest dynamics in a changing world. *Science* **368**: eaaz9463.

McDowell N**,** Pockman WT**,** Allen CD**,** Breshears DD**,** Cobb N**,** Kolb T**,** Plaut J**,** Sperry J**,** West A**,** Williams DG ***et al.*** **2008**. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.

McGregor I**,** Helcoski R**,** Kunert N**,** Tepley AJ**,** Gonzalez-Akre EB**,** Herrmann V**,** Zailaa J**,** Stovall AEL**,** Bourg NA**,** McShea WJ ***et al.*** Tree height and drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest. *Target journal: New Phytologist*.

Michaletz ST**,** Weiser MD**,** McDowell NG**,** Zhou J**,** Kaspari M**,** Helliker BR**,** Enquist BJ. **2016**. The energetic and carbon economic origins of leaf thermoregulation. *Nature Plants* **2**: 16129.

Michaletz ST**,** Weiser MD**,** Zhou J**,** Kaspari M**,** Helliker BR**,** Enquist BJ. **2015**. Plant Thermoregulation: Energetics, Trait–Environment Interactions, and Carbon Economics. *Trends in Ecology & Evolution* **30**: 714–724.

Muir CD. **2019**. Tealeaves: An R package for modelling leaf temperature using energy budgets. *AoB PLANTS* **11**.

Nakamura A**,** Kitching RL**,** Cao M**,** Creedy TJ**,** Fayle TM**,** Freiberg M**,** Hewitt CN**,** Itioka T**,** Koh LP**,** Ma K ***et al.*** **2017**. Forests and Their Canopies: Achievements and Horizons in Canopy Science. *Trends in Ecology & Evolution* **32**: 438–451.

Niinemets Ü. **2010**. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* **260**: 1623–1639.

Niinemets Ü. **2016**. Leaf age dependent changes in within-canopy variation in leaf functional traits: A meta-analysis. *J Plant Res* **129**: 313–338.

Niinemets Ü. **2006**. The controversy over traits conferring shade‐tolerance in trees: Ontogenetic changes revisited. *Journal of Ecology* **94**: 464–470.

Niinemets Ü**,** Anten NPR. **2009**. Packing the Photosynthetic Machinery: From Leaf to Canopy. In: Laisk A, Nedbal L, Govindjee, eds. Advances in Photosynthesis and Respiration. Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems. Dordrecht: Springer Netherlands, 363–399.

Niinemets Ü**,** Keenan TF**,** Hallik L. **2015**. A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist* **205**: 973–993.

Niinemets Ü**,** Kull O**,** Tenhunen JD. **2004**. Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. *Plant, Cell & Environment* **27**: 293–313.

Niinemets Ü**,** Sun Z. **2015**. How light, temperature, and measurement and growth [CO2] interactively control isoprene emission in hybrid aspen. *J Exp Bot* **66**: 841–851.

Ozanne CMP**,** Anhuf D**,** Boulter SL**,** Keller M**,** Kitching RL**,** Körner C**,** Meinzer FC**,** Mitchell AW**,** Nakashizuka T**,** Dias PLS ***et al.*** **2003**. Biodiversity Meets the Atmosphere: A Global View of Forest Canopies. *Science* **301**: 183–186.

Parker GG**,** Davis MM**,** Chapotin SM. **2002**. Canopy light transmittance in Douglas-fir–western hemlock stands. *Tree Physiol* **22**: 147–157.

Parker GG**,** Fitzjarrald DR**,** Gonçalves Sampaio IC. **2019**. Consequences of environmental heterogeneity for the photosynthetic light environment of a tropical forest. *Agricultural and Forest Meteorology* **278**: 107661.

Perkins SE**,** Alexander LV**,** Nairn JR. **2012**. Increasing frequency, intensity and duration of observed global heatwaves and warm spells. *Geophysical Research Letters* **39**.

Poorter H**,** Niinemets Ü**,** Ntagkas N**,** Siebenkäs A**,** Mäenpää M**,** Matsubara S**,** Pons T. **2019**. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytol.* **223**: 1073–1105.

Rey-Sánchez A**,** Slot M**,** Posada J**,** Kitajima K. **2016**. Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research* **71**: 75–89.

Roberts J**,** Cabral OMR**,** Aguiar LFD. **1990**. Stomatal and Boundary-Layer Conductances in an Amazonian terra Firme Rain Forest. *The Journal of Applied Ecology* **27**: 336.

Rollinson CR**,** Alexander MR**,** Dye AW**,** Moore DJP**,** Pederson N**,** Trouet V. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. *Ecology* **n/a**: e03264.

Sack L**,** Melcher PJ**,** Liu WH**,** Middleton E**,** Pardee T. **2006**. How strong is intracanopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* **93**: 829–839.

Sastry A**,** Guha A**,** Barua D. **2018**. Leaf thermotolerance in dry tropical forest tree species: Relationships with leaf traits and effects of drought. *AoB PLANTS* **10**.

Senf C**,** Pflugmacher D**,** Zhiqiang Y**,** Sebald J**,** Knorn J**,** Neumann M**,** Hostert P**,** Seidl R. **2018**. Canopy mortality has doubled in Europe’s temperate forests over the last three decades. *Nature Communications* **9**: 4978.

Senf C**,** Seidl R. **2020**. Mapping the forest disturbance regimes of Europe. *Nature Sustainability*: 1–8.

Sharkey TD**,** Monson RK. **2014**. The future of isoprene emission from leaves, canopies and landscapes. *Plant, Cell & Environment* **37**: 1727–1740.

Smith MN**,** Stark SC**,** Taylor TC**,** Ferreira ML**,** Oliveira E de**,** Restrepo‐Coupe N**,** Chen S**,** Woodcock T**,** Santos DB dos**,** Alves LF ***et al.*** **2019**. Seasonal and drought-related changes in leaf area profiles depend on height and light environment in an Amazon forest. *New Phytologist* **222**: 1284–1297.

Stark SC**,** Breshears DD**,** Aragón S**,** Villegas JC**,** Law DJ**,** Smith MN**,** Minor DM**,** Assis RL de**,** Almeida DRA de**,** Oliveira G de ***et al.*** **2020**. Reframing tropical savannization: Linking changes in canopy structure to energy balance alterations that impact climate. *Ecosphere* **11**: e03231.

Stokes VJ**,** Morecroft MD**,** Morison JIL. **2006**. Boundary layer conductance for contrasting leaf shapes in a deciduous broadleaved forest canopy. *Agricultural and Forest Meteorology* **139**: 40–54.

Stovall AEL**,** Shugart H**,** Yang X. **2019**. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**: 4385.

Thom D**,** Sommerfeld A**,** Sebald J**,** Hagge J**,** Müller J**,** Seidl R. **2020**. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agricultural and Forest Meteorology* **291**: 108066.

Tymen B**,** Vincent G**,** Courtois EA**,** Heurtebize J**,** Dauzat J**,** Marechaux I**,** Chave J. **2017**. Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science* **74**: 32.

von Arx G**,** Dobbertin M**,** Rebetez M. **2012**. Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agricultural and Forest Meteorology* **166-167**: 144–155.

Yang PC**,** Black TA**,** Neumann HH**,** Novak MD**,** Blanken PD. **1999**. Spatial and temporal variability of CO2 concentration and flux in a boreal aspen forest. *Journal of Geophysical Research: Atmospheres* **104**: 27653–27661.

Zellweger F**,** Coomes D**,** Lenoir J**,** Depauw L**,** Maes SL**,** Wulf M**,** Kirby KJ**,** Brunet J**,** Kopecký M**,** Máliš F ***et al.*** **2019**. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe (A Algar, Ed.). *Global Ecology and Biogeography* **28**: 1774–1786.

Zellweger F**,** De Frenne P**,** Lenoir J**,** Vangansbeke P**,** Verheyen K**,** Bernhardt-Römermann M**,** Baeten L**,** Hédl R**,** Berki I**,** Brunet J ***et al.*** **2020a**. Forest microclimate dynamics drive plant responses to warming. *Science* **368**: 772–775.

Zellweger F**,** Frenne PD**,** Lenoir J**,** Vangansbeke P**,** Verheyen K**,** Bernhardt-Römermann M**,** Baeten L**,** Hédl R**,** Berki I**,** Brunet J ***et al.*** **2020b**. Response to Comment on ‘Forest microclimate dynamics drive plant responses to warming’. *Science* **370**.

Zhang J-L**,** Poorter L**,** Hao G-Y**,** Cao K-F. **2012**. Photosynthetic thermotolerance of woody savanna species in China is correlated with leaf life span. *Annals of Botany* **110**: 1027–1033.