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RESEARCH ARTICLE

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Respiratory temperature responses of tropical conifers differ with leaf morphology

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Abstract

1. Photosynthetic traits suggest that shade tolerance may explain the contrasting success of two conifer taxa, Podocarpaceae and Pinaceae, in tropical forests. Needle-leaved species from *Pinus* (Pinaceae) are generally absent from tropical forests, whereas *Pinus krempfii*, a flat-leaved pine, and numerous flat-leaved Podocarpaceae are abundant. Respiration (*R*) traits may provide additional insight into the drivers of the contrasting success of needle- and flat-leaved conifers in tropical forests.
2. We measured the short-term respiratory temperature (RT) response between 10 and 50°C and foliar morphological traits of three needle- and seven flat-leaved conifer species coexisting in a tropical montane forest in the Central Highlands of Vietnam containing notable conifer diversity. We fit a lognormal polynomial model to each RT curve and extracted the following three parameters: *a* (basal *R*), and *b* and *c* (together describing the shape of the response).
3. Needle-leaved species (*Pinus kesiya*, *Pinus dalatensis* and *Dacrydium elatum*) had higher rates of area-based *R* at 25°C ($R_{25\text{-area}}$) as well as higher area-based modelled basal respiration (*a*) than flat-leaved species (*P. krempfii*, *Podocarpus neriifolius*, *Dacrycarpus imbricatus*, *Nageia nana*, *Taxus wallichiana*, *Keteeleria evelyniana* and *Fokienia hodginsii*). No significant differences were found between needle- and flat-leaved species in mass-based R_{25} ($R_{25\text{-mass}}$) or in the shape of the RT response (*b* and *c*); however, interspecific differences in $R_{25\text{-mass}}$, *R* at nighttime temperature extremes ($R_{4.1}$ and $R_{20.6}$) and leaf traits were apparent.
4. Differences in $R_{25\text{-area}}$ and *a* suggest that needle-leaved foliage may be more energetically costly to maintain than flat-leaved foliage, providing new insight and additional support for the hypothesis that shade tolerance is an important driver of Podocarpaceae success and Pinaceae absence in the majority of tropical forests.
5. Interspecific differences in $R_{25\text{-mass}}$ and leaf traits highlight that varying ecological strategies are employed by conifers to coexist and survive in the Central Highlands

of Vietnam. Ultimately, these data further our understanding of current conifer biogeographical distributions and underscore the need for additional studies to elucidate the effects of extreme temperature events on the continued survival of conifers in this unique forest.

KEYWORDS

conifers, respiration, temperature, tropical montane forests

1 | INTRODUCTION

Arising more than 300 million years ago, conifers once dominated the global vegetated landscape (Farjon & Filer, 2013). Their long evolutionary history witnessed adaptation to a wide variety of climates: yet, the radiation of angiosperms beginning in the Early Cretaceous produced a shift in biodiversity that coincided with the disappearance of conifer species from many ecosystems; most notably from the tropics (Berendse & Scheffer, 2009; Biffin et al., 2012; Dalling et al., 2016). Hypotheses for the absence of conifers from lowland tropical forests suggest conifers are unable to compete with fast angiosperm growth rates due to vascular constraints on maximum leaf size, and inefficient hydraulic transport (Bond, 1989; Brodribb et al., 2012; Lusk et al., 2003). Comparisons among conifer families with different biogeographical histories and leaf shapes, most notably between Laurasian Pinaceae and Gondwanan Podocarpaceae, further suggest that shade intolerance and the lack of a flattened leaf morphology in Pinaceae led to their exclusion from the majority of tropical ecosystems (Brodribb & Feild, 2008; Lusk, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021). Pinaceae have narrow, needle-like leaves with the exception of two flat-leaved taxa, *Pinus krempfii*, an endemic to the Central Highlands of Vietnam (Buchholz, 1951; Lecomte, 1921) and *Keteleeria* (Brodribb et al., 2012). In contrast, Podocarpaceae are a predominantly flat-leaved conifer family that only colonized the tropics in the last 60 million years, after the rise of angiosperms in tropical forests (Morley, 2011; Quiroga et al., 2016).

Flat leaves are an important characteristic of shade-tolerant species, as a greater leaf surface area allows for greater capture of photosynthetically active radiation in light-limited environments such as sub-canopy tropical forests (Brodribb, 2011; Brodribb & Hill, 1997; Lusk, 2002). Additional support for the importance of shade-tolerant characteristics to conifer survival in the tropics comes from photosynthetic traits. *Pinus* have higher rates of maximum photosynthesis than Podocarpaceae (Brodribb & Feild, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021), higher rates of rubisco carboxylation (V_{cmax}) than Podocarpaceae (Schmiege, Buckley, Stevenson, Cuong, et al., 2021), but similar rates of electron transport (J_{max}) to Podocarpaceae (Schmiege, Buckley, Stevenson, Cuong, et al., 2021). These findings suggest that flat-leaved Podocarpaceae may invest more in capturing light energy (J_{max}) than in carboxylation (V_{cmax}). Ultimately, Schmiege, Buckley, Stevenson, Cuong, et al. (2021) highlight a potentially critical link between photosynthetic physiology, leaf morphology and shade tolerance that may drive the comparative success of Podocarpaceae and failure of Pinaceae to survive in tropical forests.

The aforementioned studies greatly advance our understanding of the photosynthetic traits and mechanisms contributing to conifer survival in tropical forests; however, few studies have assessed the links between leaf morphology and respiration (*R*) (but see Schmiege, Buckley, Stevenson, Cuong, et al. (2021). *R*, a fundamental process contributing to cell and organismal function, might also contribute to the shade tolerance and relative success of conifer species in the tropics. Plant *R* supports the growth and maintenance of all plant tissues and accounts for 50% of all carbon released to the atmosphere (Atkin et al., 2007). *R* correlates with a number of leaf traits including photosynthetic carbon assimilation, foliar nitrogen, leaf mass per area (LMA) and leaf life span (Reich et al., 1998; Wright et al., 2004). These linkages are likely due to demands for respiratory products in processes such as photosynthesis, phloem-loading and protein turn-over (Atkin & Tjoelker, 2003; Noguchi & Yoshida, 2008). Ultimately, the differing demands of these processes are manifest in variation of *R* across species, plant functional types (PFTs), populations and growth forms (Atkin et al., 2015; Patterson et al., 2018; Turnbull et al., 2005; Wright et al., 2006). *R* is also an important characteristic contributing to tolerance of low-light conditions in shade-tolerant species. Many shade-tolerant species maintain a positive carbon balance in low-light environments by decreasing both their light compensation points and their whole-plant respiratory losses (Givnish, 1988; Valladares & Niinemets, 2008).

Mechanistically, temperature (*T*) is one of the strongest environmentally determinant drivers of the respiratory rate (Atkin & Tjoelker, 2003). Consequently, understanding the response of *R* to *T* across both short and long time-scales is critical to the accurate predictions of *R* (Huntingford et al., 2017). Here we focus on the short-term response of *R* to *T*. Mechanistically, over the short term, *R* is strongly controlled by *T* because respiratory enzymatic reaction rates increase with *T* over the ecologically relevant range of ambient temperatures (Atkin & Tjoelker, 2003). Increases in *T* lead to a nonlinear increase in *R*, a response that has been accurately modelled by log-transforming *R* and fitting a second-order polynomial model to the response (Heskel et al., 2016). Furthermore, a large global study of respiratory temperature (*RT*) response curves and *R* at a common measurement *T* of 25°C across global biomes and PFTs has highlighted two important findings that may have bearing on our examination of the impacts of leaf morphology and *R* on conifer survival in tropical forests: first, leaf *R* at a common measurement *T* varies across PFTs (e.g. with higher *R* in needle-leaved evergreens than broad-leaved evergreens), and second, the function describing the rise in *R* with *T* is the same across plants, regardless of growth environment or PFT (Atkin et al., 2015; Heskel et al., 2016).

In this study, we examine the respiratory rates of 10 tropical conifers with different leaf morphologies (flat or needle-like) and biogeographical histories that coexist in a single location in the Central Highlands of Vietnam. This tropical location is unique in its conifer diversity because it contains conifer species from four families representing a diversity of leaf morphologies. We use this diversity to assess two questions: first, whether metabolic physiology and morphology correlate with greater persistence of broad-leaved conifers compared to needle-leaved conifers in the majority of tropical forests; and second, whether species' traits reveal similar or different life-history strategies permitting the coexistence of these diverse conifers in this unique tropical location. Our dataset provides some of the first data on the *RT* response in an important but underrepresented group of tropical montane species, allowing for the analysis of species-specific differences in *RT* responses and relationships with leaf traits. We hypothesize the following: (1) Shade-intolerant needle-leaved evergreen conifers will have higher *R* measured at a common *T* of 25°C than broad-leaved evergreen conifers following previously observed differences in photosynthetic traits of Pinaceae and Podocarpaceae species (Brodribb & Feild, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021) and differences across PFTs in Heskel et al. (2016); (2) differences in *R* will correlate to leaf traits following the leaf economics spectrum (Wright et al., 2004) and (3) the shape of the overall *RT* response will not differ between needle-leaved and broad-leaved conifers following the findings of Heskel et al. (2016).

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in the Central Highlands of Vietnam in Bidoup Nui Ba National Park near the city of Dalat in Lam Dong province (12°08′1.4676″N latitude, 108°32′1.2192″E longitude). Approximately 1,500 m a.s.l., this location is part of the Annamite mountain range where the Laurasian and Gondwanan supercontinents converged (Gupta, 2005). The location has a mean annual temperature of 18°C (Schmiege, Buckley, Stevenson, Cuong, et al., 2021; Figure 1). It receives approximately 1,800 mm of precipitation annually, the majority of which falls during the Southeast Asian Summer Monsoon in May through October (Wang & LinHo, 2002; Figure 1).

The Central Highlands of Vietnam contain large conifer diversity, and Bidoup Nui Ba National Park itself contains 13 conifers from four families (Loc et al., 2017). We measured 10 of 13 total species (Table 1), the majority of which grow in a 20 ha plot of primary forest located near the Giang Ly Forest Station and weather station at an elevation of 1,500 m (12°11′58.6314″N latitude, 108°40′52.284″E longitude). Podocarpaceae species included *Podocarpus neriifolius*, *Dacrycarpus imbricatus*, *Dacrydium elatum* and *Nageia nagi*. Pinaceae species included *Pinus kesiya*, *Pinus dalatensis*, *Pinus krempfii* and *Keteleeria evelyniana*. *Fokienia hodginsii* from the Cupressaceae, and *Taxus wallichiana* from the Taxaceae were also measured. Of these species, three are needle-leaved: *P. dalatensis*, *P. kesiya* and *D. elatum*. All others have a flattened leaf morphology. All Podocarpaceae, in addition to *P. krempfii*, *P. dalatensis*, *K. evelyniana*, *F. hodginsii* and *T. wallichiana* grow in the forest interior (Farjon & Filer, 2013). *P. kesiya* grows in monoculture stands at the forest edge where fires and human disturbance are more common (Agee, 1998; Goldammer & Penafiel, 1990). Of

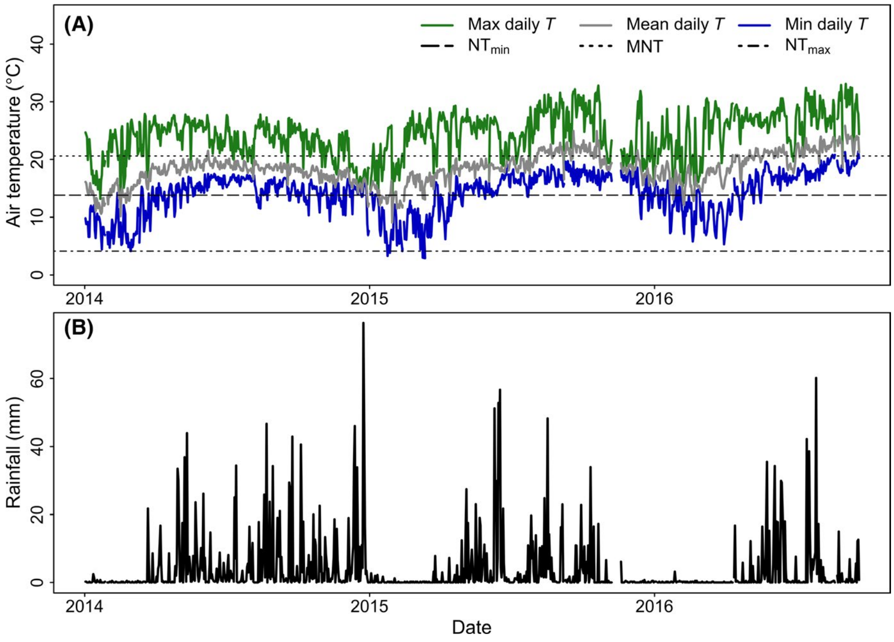

FIGURE 1 Mean, maximum and minimum daily temperature (*T*; A) and total daily rainfall (B) from the nearest weather station at Giang Ly. The dashed line represents the mean nighttime temperature (MNT; 13.8°C), the dotted line represents the nighttime temperature maximum calculated as the mean maximum nighttime temperature of the warmest 3-day period (NT_{max}; 20.6°C), and the dot-dashed line represents the nighttime temperature minimum calculated as the mean minimum nighttime temperature of the coldest 3-day period (NT_{min}; 4.1°C) from the nearby Giang Ly meteorological station 2014–2016

TABLE 1 Conifer species for which *RT* response curves were measured in the Central Highlands of Vietnam. Species abbreviations are in parentheses. Species are categorized according to their leaf morphology. For each species, the mean and standard error (*SE*) of the DBH (cm) of the measured trees are included along with brief species' descriptions compiling information from Coomes and Bellingham (2011), Farjon (2017), Loc et al. (2017) and Schmiege, Buckley, Stevenson, Cuong, et al. (2021)

Needle-leaved species	Family	DBH (*SE*)	Description
Pinus kesiya (PIKE)	Pinaceae	33.86 (3.46)	Shade-intolerant pioneer that is found in monoculture stands or at forest edges. Fire resistant
Pinus dalatensis (PIDA)	Pinaceae	20.48 (3.52)	Shade intolerant requiring disturbance to establish. Canopy emergent
Dacrydium elatum (DAEL)	Podocarpaceae	22.29 (4.36)	Common in open conditions but also found infrequently in moist rainforest with only occasional regeneration. Likely shade intolerant
Flat-leaved Species	**Family**	**DBH (*SE*)**	**Description**
Keteleeria evelyniana (KEEV)	Pinaceae	24.78 (3.25)	Generally shade intolerant, canopy tree with narrow but flattened needles
Pinus krempfii (PIKR)	Pinaceae	17.10 (2.86)	Likely shade tolerant with abundant seedlings under adult trees. Grows to be canopy emergent
Podocarpus neriifolius (PONE)	Podocarpaceae	11.59 (1.18)	Shade-tolerant canopy tree with occasional regeneration
Dacrycarpus imbricatus (DAIM)	Podocarpaceae	11.58 (2.44)	Canopy tree with shade-tolerant seedlings and occasional regeneration
Nageia nagi (NANA)	Podocarpaceae	17.44 (2.87)	Shade-tolerant tree but may become a canopy dominant
Fokienia hodginsii (FOHO)	Cupressaceae	49.62 (5.97)	Moderately shade-tolerant tree that can form pure stands. Seed regeneration is uncommon
Taxus wallichiana (TAWA)	Taxaceae	42.74 (15.32)	Lower canopy shade-tolerant tree with occasional regeneration

these species, two were not found near Giang Ly: *K. evelyniana* and *T. wallichiana*. Individuals of these two species were located 40 km west of the Giang Ly forest station. All species, regardless of location, grew at similar elevations of approximately 1,500 m. Additional species' information are shown in Table 1.

2.2 | Climate data

Meteorological data, including air temperature and rainfall, were collected from the weather station at the Giang Ly Forest Station adjacent to the forest plot between January 2014 and October 2016. From these data, we assessed the mean annual nighttime temperature (MNT; °C) using methods similar to the calculation of mean annual temperature (MAT) in Fick and Hijmans (2017) and O'Donnell and Ignizio (2012). MNT was calculated using the following equation:

$$\mathrm{MNT} = \frac{\sum_{i=1}^{i=12} T\mathrm{avg}_i}{12},$$

in which i is the month, and $T\mathrm{avg}_i$ is the average of the maximum and minimum monthly nighttime temperature. Current nighttime temperature extremes in the Central Highlands were also determined by calculating the mean maximum nighttime air temperature of the warmest 3-day period ($\mathrm{NT}_{\mathrm{max}}$) and the mean minimum nighttime air temperature of the coldest 3-day period ($\mathrm{NT}_{\mathrm{min}}$) following O'Sullivan et al. (2017).

2.3 | Respiration temperature curves

For *RT* measurements, we selected branches from the upper canopies of 4–6 adult trees of each of the 10 conifer species (Table 1). Given the complex canopy structure and local topography, we minimized undocumented variance in ambient light conditions that would exist in a complex understorey light environment by choosing branches that experienced exposure to direct radiation. Branches were transported to the laboratory, and stems were recut underwater and then kept in water until measurements were completed. All measurements were made within 2 days of cutting branches. Fully expanded leaves were selected from each branch sample and cut to measure the RT response.

Respiration temperature curves were measured using a custom-designed system with the following components: a custom-built leaf chamber attached to a temperature controller (TE Technology CP-121 Thermoelectric Peltier Cooling Unit) and an infrared gas analyzer (LI-6400xt; LiCor). Airflow through the chamber was set at 500 ml/min while a centrifugal fan ensured a well-mixed environment. Reference CO_2 was set to 400 ppm during the measurements. To avoid condensation at low temperatures, the incoming air was dried with the Li-6400XT desiccant column and leaf transpiration was allowed to humidify the air during the measurements as in O'Sullivan et al. (2013). Leaf temperature inside the cuvette was measured using a fine wire thermocouple. Leaves in the chamber were dark-adapted by covering the cuvette with a dark cloth. Leaf temperature was lowered to ~10°C and then ramped continuously to ~50°C at a rate of 1°C per minute. Concurrently, respiratory rates were recorded every 20 s during the temperature ramp using a LI-6400xt infrared gas analyzer according to methods delineated by Heskel et al. (2016) and O'Sullivan et al. (2013).

2.4 | Analysis of RT curves and R_{25}

Respiration temperature curves were analysed by natural log transforming *R* and fitting a second-order polynomial to the relationship between ln*R* and *T* (Heskel et al., 2016) according to the equation:

$$\ln R = a + bT + cT^2,$$

where *a* represents the basal respiration (*y*-intercept), and *b* and *c* together describe the slope and the curvature of the response, respectively (Heskel et al., 2016). From these fitted curves, we extracted respiration at 25°C (R_{25}), the current mean nighttime temperature (MNT; 13.8°C, $R_{13.8}$) and the current nighttime temperature extremes ($\mathrm{NT_{min}}$, 4.1°C, $R_{4.1}$; $\mathrm{NT_{max}}$, 20.6°C, $R_{20.6}$, respectively). For $\mathrm{NT_{min}}$, $R_{4.1}$ was extrapolated from the fit of the model to the *RT* curves because the lowest measured temperature for the *RT* curves was 10°C.

2.5 | Leaf trait measurements

All leaves measured in the *RT* curves were photographed to measure projected leaf area ($\mathrm{cm^2}$) using ImageJ (Schnieder et al., 2012). All photographs were visually examined to minimize artefacts caused by shadows. These leaves were stored in coin envelopes and dried in an oven at 65°C for at least 48 hr, after which they were weighed for leaf dry mass (g). Leaf mass per area (LMA; $\mathrm{g/cm^2}$) was calculated and used to convert area-based respiratory fluxes to mass-based fluxes and to convert mass-based nutrient concentrations to area-based estimates. We measured % carbon and % nitrogen of the leaf samples by grinding the dried leaves into a powder using a ball mill (SPEX 8000 Mixer/Mill), weighing 2–4 mg of this powder into tin capsules, and running these tin capsules through a carbon–nitrogen flash analyzer (CE Elantech). From the resulting percentages, leaf nitrogen per mass ($\mathrm{N_{mass}}$; $\mathrm{mg_N/g}$), leaf carbon per mass ($\mathrm{C_{mass}}$; $\mathrm{mg_C/g}$), the carbon to nitrogen ratio (C:N), leaf nitrogen per area ($\mathrm{N_{area}}$; $\mathrm{mg_N/cm^2}$) and leaf carbon per area ($\mathrm{C_{area}}$; $\mathrm{mg_C/cm^2}$) were calculated.

2.6 | Statistical analyses

We assessed differences between species and leaf morphologies (flat or needle leaf shape) for all parameters, including the polynomial model parameters: *a*, *b* and *c* on both an area and a mass basis (a_{area}, a_{mass}, b_{area}, b_{mass}, c_{area} and c_{mass}); R_{25} on an area-, mass- and per N basis ($R_{25\text{-area}}$, $R_{25\text{-mass}}$ and $R_{25\text{-perN}}$, respectively), area- and mass-based $R_{13.8}$, $R_{20.6}$ and $R_{4.1}$; and leaf traits including $\mathrm{C_{mass}}$, $\mathrm{C_{area}}$, $\mathrm{N_{mass}}$, $\mathrm{N_{area}}$, C:N ratio and LMA using one-way analysis of variance and Tukey HSD Post-Hoc with a significance value of 0.05. We calculated means, confidence intervals and standard errors and transformed all traits to fulfil assumptions of normality, as necessary. For comparisons between leaf morphologies, we used a linear mixed effects modelling framework to incorporate species as a random effect (using the LME4 package; Bates et al., 2015). As a result, for leaf morphology, pairwise comparisons were made via Tukey Post Hoc using emmeans (Lenth, 2020), and the marginal coefficient of determination (variance explained by the fixed effects; r_m^2) and the conditional coefficient of determination (variance explained by the fixed and the random effects; r_c^2) were calculated in the MuMIn package (Bartoń, 2020).

Relationships between $R_{25\text{-area}}$ and $\mathrm{N_{area}}$, and $R_{25\text{-mass}}$ and $\mathrm{N_{mass}}$ were assessed using linear mixed-effects models with species as a random effect using LME4 (Bates et al., 2015) with LMERTEST to retrieve *p* values (Kuznetsova et al., 2017) and MuMIn to calculate r_m^2 and r_c^2 (Bartoń, 2020). Data analysis took place in R v. 3.6.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Effects of temperature on respiration for the conifers from Vietnam

Mean area- and mass-based *a*, *b* and *c* describing the polynomial model fit to the *RT* response differed significantly among conifer species (Figure 2; Tables 2 and 3), as did $R_{25\text{-area}}$, $R_{25\text{-mass}}$ and $R_{25\text{-perN}}$ (Figure 3; Table 3). Of particular note is the fact that *P. krempfii*, the endemic flat-leaved pine, demonstrated much lower $R_{25\text{-area}}$ than the other Pinaceae (*K. evelyniana*, *P. kesiya* and *P. dalatensis*; Figure 3A); *D. elatum*, a needle-leaved Podocarpaceae had higher $R_{25\text{-area}}$ than all other Podocarpaceae (*D. imbricatus* and *P. neriifolius*) except for *N. nagi* which had a wide range of *R* values (Figure 3A). Interestingly, *K. evelyniana*, the other flat-leaved Pinaceae, had similar $R_{25\text{-area}}$ to the other needle-leaved species (Figure 3A). $R_{25\text{-mass}}$ and $R_{25\text{-perN}}$ were also significantly different across Vietnamese conifer species, but differences did not follow the same patterns as $R_{25\text{-area}}$. *P. dalatensis* demonstrated the highest $R_{25\text{-mass}}$ (Figure 3D), and *P. dalatensis* and *K. evelyniana* demonstrated the highest $R_{25\text{-perN}}$ (Figure 3F).

When species were grouped by leaf morphology, there were no significant differences between needle- and flat-leaved species in area- or mass-based *b* and *c* describing the shape of the *RT* curves (Figure 2; Tables 2 and 3). There were also no significant differences between needle- and flat-leaved species for a_{mass} (Figure 2D; Tables 2 and 3). However, needle-leaved species had higher a_{area} than flat-leaved species (Figure 2B; Tables 2 and 3). When examining differences in R_{25} by leaf morphology, needle-leaved species had significantly higher $R_{25\text{-area}}$ than flat-leaved species (Figure 3A; Table 3). However, there were no significant differences in $R_{25\text{-mass}}$ or $R_{25\text{-perN}}$ according to leaf morphology (Figure 3B,C; Table 3).

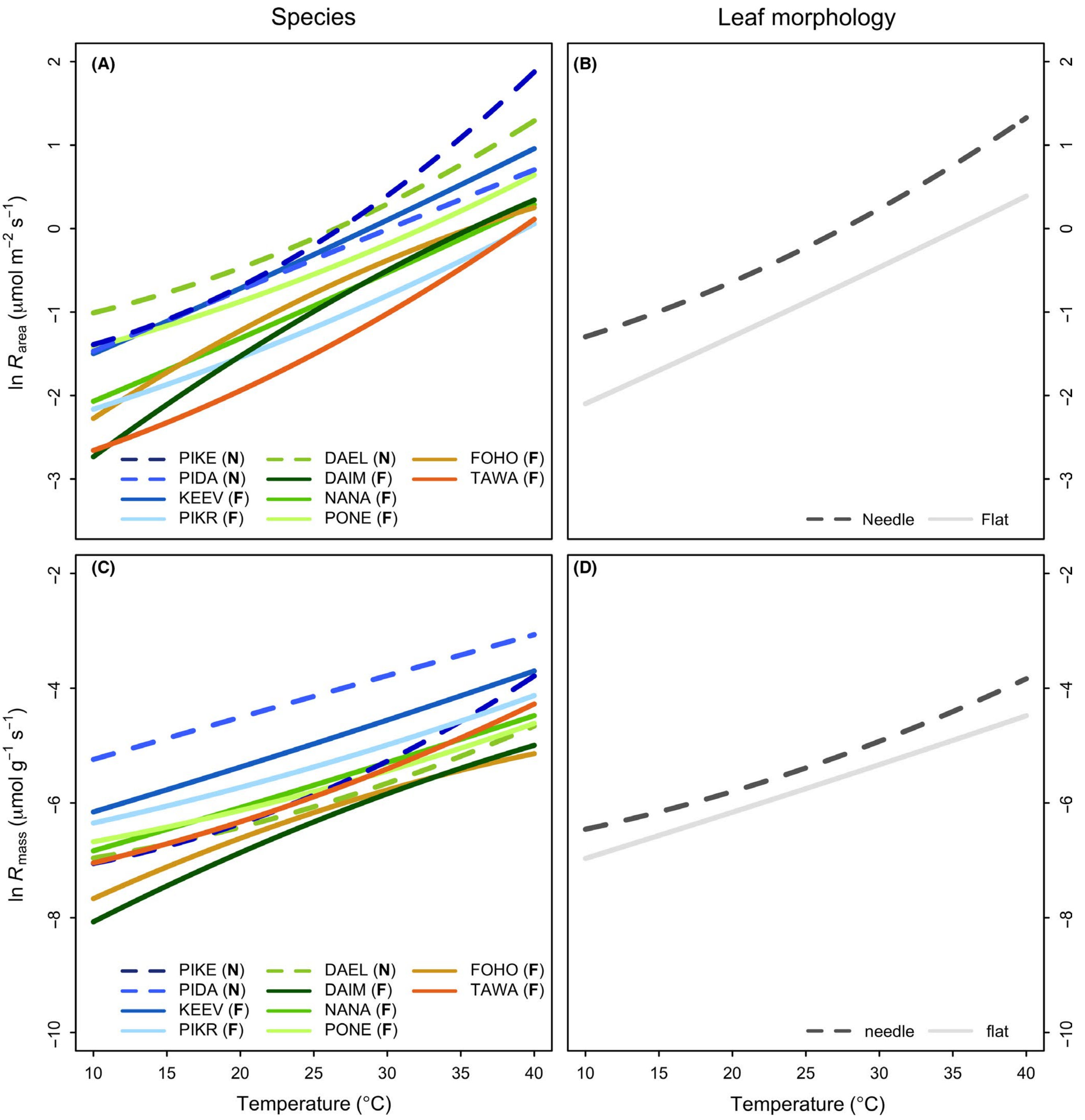

FIGURE 2 Modelled *RT* curves for species and leaf morphologies of the Vietnamese conifers on an area (A, B) and a mass (C, D) basis created using the mean *a*, *b* and *c* polynomial coefficients from Table 2. Species from the Pinaceae are in shades of blue, from the Podocarpaceae in shades of green, from the Cupressaceae in yellow and the Taxaceae in orange. Needle-leaved species are marked by dashed lines and (N) after each species abbreviation. Flat-leaved species are marked by solid lines and (F) after each species abbreviation

3.2 | Leaf traits of the conifers from the central highlands of Vietnam

Mean values of C_{mass}, N_{mass}, C_{area}, N_{area}, C:N ratio and LMA were significantly different among Vietnamese conifer species, but not when species were grouped by leaf morphology (Figure 4; Table 3). Differences were species specific but correlated among leaf traits. For example, *P. kesiya*, *D. elatum*, *F. hodginsii* and *P. neriifolius* all seemed to have higher LMA, lower N_{mass}, higher C:N and higher N_{area}. In contrast, *P. dalatensis*, *P. krempfii* and to some extent, *K. evelyniana* and *T. wallichiana* all had lower LMA, higher N_{mass}, lower C:N and lower N_{area}. *D. imbricatus* and *N. nagi* seemed to fall between the two groups of species.

TABLE 2 Mean estimates and 95% confidence intervals for the basal respiratory rates (*a*), as well as the slope and curvature of the response (*b* and *c*) describing the fit of the polynomial model to the *RT* curves for conifer species and for leaf morphology. Significant differences between groups are marked by different letters ($p < 0.05$)

Species	***a***	**95% CI**	***b***	**95% CI**	***c***	**95% CI**
$\ln RT_{area}$						
PIKE (N)	-1.6913^{de}	[−2.3377, −1.0449]	0.0105^{a}	[−0.0408, 0.0618]	0.0020^{d}	[0.0010, 0.0030]
PIDA (N)	-2.2167^{cde}	[−2.9248, −1.5086]	0.0752^{ab}	[0.0190, 0.1314]	-0.000^{abc}	[−0.0012, 0.0010]
DAEL (N)	-1.3166^{e}	[−2.0247, −0.6085]	0.0193^{a}	[−0.0369, 0.0755]	0.0011^{cd}	[0.0000, 0.0023]
KEEV (F)	-2.2430^{cde}	[−2.9511, −1.5348]	0.0726^{ab}	[0.0164, 0.1288]	0.0002^{abc}	[−0.0009, 0.0013]
PIKR (F)	-2.6668^{bcd}	[−3.3749, −1.9587]	0.0443^{a}	[−0.0119, 0.1005]	0.0006^{abcd}	[−0.0005, 0.0017]
DAIM (F)	-2.7928^{bcd}	[−3.5845, −2.0011]	0.0708^{ab}	[0.0080, 0.1336]	0.0002^{abc}	[−0.0011, 0.0014]
NANA (F)	-1.8265^{de}	[−2.4729, −1.1800]	0.0335^{a}	[−0.0178, 0.0848]	0.0007^{bcd}	[−0.0003, 0.0017]
PONE (F)	-4.1192^{a}	[−4.8273, −3.4111]	0.1476^{b}	[0.0914, 0.2038]	-0.0009^{ab}	[−0.0020, 0.0002]
FOHO (F)	-3.5357^{ab}	[−4.2439, −2.8276]	0.1366^{b}	[0.0804, 0.1928]	-0.0010^{a}	[−0.0021, 0.0001]
TAWA (F)	-3.1677^{abc}	[−3.8758, −2.4596]	0.0407^{a}	[−0.0155, 0.0969]	0.0010 cd	[−0.0001, 0.0021]
$\ln RT_{mass}$						
PIKE (N)	-7.3563^{b}	[−7.9817, −6.7310]	0.0105^{a}	[−0.0408,0.0618]	0.0020^{d}	[0.0010, 0.0030]
PIDA (N)	-5.9887^{c}	[−6.6737, −5.3036]	0.0752^{ab}	[0.0190, 0.1314]	-0.0001^{abc}	[−0.0012, 0.0010]
DAEL (N)	-7.2673^{b}	[−7.9523, −6.5822]	0.0193^{a}	[−0.0369, 0.0755]	0.0011 cd	[0.0000, 0.0023]
KEEV (F)	-6.9013^{bc}	[−7.5864, −6.2163]	0.0726^{ab}	[0.0164, 0.1288]	0.0002^{abc}	[−0.0009, 0.0013]
PIKR (F)	-6.8528^{bc}	[−7.5378, −6.1677]	0.0443^{a}	[−0.0119, 0.1005]	0.0006^{abcd}	[−0.0005, 0.0017]
DAIM (F)	-7.5582^{b}	[−8.3241, −6.7923]	0.0708^{ab}	[0.0080, 0.1336]	0.0002^{abc}	[−0.0011, 0.0014]
NANA (F)	-7.0830^{b}	[−7.7083, −6.4576]	0.0335^{a}	[−0.0178, 0.0848]	0.0007^{bcd}	[−0.0003, 0.0017]
PONE (F)	-9.4573^{a}	[−10.1424, −8.7723]	0.1476^{b}	[0.0914, 0.2038]	-0.0009^{ab}	[−0.0020, 0.0002]
FOHO (F)	-8.9286^{a}	[−9.6136, −8.2435]	0.1366^{b}	[0.0804, 0.1928]	-0.0010^{a}	[−0.0021, 0.0001]
TAWA (F)	-7.5552^{b}	[−8.2402, −6.8702]	0.0407^{a}	[−0.0155, 0.0969]	0.0010 cd	[−0.0001, 0.0021]
Leaf morphology	***a***	**95% CI**	***b***	**95% CI**	***c***	**95% CI**
$\ln RT_{area}$						
Flat	-2.9049^{a}	[−3.6436, −2.1661]	0.0779^{a}	[0.0323, 0.1234]	0.0001^{a}	[−0.0008, 0.0010]
Needle	-1.7412^{b}	[−2.8692, −0.6133]	0.0347^{a}	[−0.0348, 0.1043]	0.0010^{a}	[−0.0003, 0.0024]
$\ln RT_{mass}$						
Flat	-7.7618^{a}	[−8.7676, −6.756]	0.0779^{a}	[0.0323, 0.1234]	0.0001^{a}	[−0.0008, 0.0010]
Needle	-6.8723^{a}	[−8.4083, −5.3363]	0.0347^{a}	[−0.0348, 0.1043]	0.0010^{a}	[−0.0003, 0.0024]

3.3 | Relationships between respiration and leaf traits

We found statistically significant relationships between $R_{25\text{-area}}$ and N_{area}, and $R_{25\text{-mass}}$ and N_{mass} (Figure 5). The variance explained by the fixed effects was much larger in the relationship between $R_{25\text{-area}}$ and N_{area} than $R_{25\text{-mass}}$ and N_{mass} (r^2_m = 0.29 as opposed to 0.13). However, the variances explained by the full models including species as a random effect were the same for $R_{25\text{-mass}}$ versus N_{mass} and $R_{25\text{-area}}$ versus N_{area} (r^2_c = 0.87). Significant relationships were also found between $R_{25\text{-area}}$ or $R_{25\text{-mass}}$ and LMA. Both r^2_m and r^2_c were greater in the relationship between $R_{25\text{-area}}$ and LMA than in the relationship between $R_{25\text{-mass}}$ and LMA (Figure 4). Lastly, significant relationships were found between R_{25} and the area- and mass-based *RT* polynomial coefficients except for $R_{25\text{-mass}}$ versus a_{mass} and $R_{25\text{-area}}$ versus c_{area} (see Table S1). The only significant relationship between N and the *RT* polynomial coefficients was between N_{area} and a_{area} (Table S1).

3.4 | Impacts of nighttime temperatures on the respiration of Vietnamese conifers

In addition to examining *R* at a common temperature of 25°C, we also examined the respiratory fluxes of conifers under the temperature range these species are known to experience (Figures 1 and 6; Table 4). As *R* occurs during non-daylight hours, we calculated the mean nighttime temperature as well as the nighttime temperature

TABLE 3 One-way ANOVA model results for *RT* polynomial coefficients and respiration and leaf traits for the Vietnamese conifers by species and leaf morphology

	Species				Leaf morphology				
	F value	Pr > *F*	r^2	*df*	*F* value	Pr > *F*	r^2_m	r^2_c	*df*
Polynomial coefficients ($\ln RT_{area}$)									
a	13.78	<0.001	0.70	9,41	5.62	0.045	0.13	0.8	1, 8.02
b	6.15	<0.001	0.48	9,41	2.03	0.192	0.11	0.52	1, 7.97
c	6.51	<0.001	0.5	9,41	2.43	0.158	0.13	0.53	1, 7.99
Polynomial coefficients ($\ln RT_{mass}$)									
a	19.11	<0.001	0.77	9,41	1.77	0.22	0.13	0.8	1, 7.98
b	6.15	<0.001	0.48	9,41	2.03	0.192	0.11	0.52	1, 7.97
c	6.51	<0.001	0.5	9,41	2.43	0.158	0.13	0.53	1, 7.99
Respiration									
$R_{25\text{-area}}$	11.15	<0.001	0.65	9,41	7.54	0.025	0.06	0.88	1, 7.96
$R_{25\text{-mass}}$	33.60	<0.001	0.85	9,41	0.72	0.421	0.06	0.88	1, 7.99
$R_{25\text{-perN}}$	28.05	<0.001	0.83	9,41	2.26	0.171	0.06	0.88	1, 7.98
Leaf traits									
C_{mass}	11.97	<0.001	0.66	9,41	3.04	0.12	0.18	0.7	1, 7.93
N_{mass}	29.98	<0.001	0.84	9,41	0.45	0.523	0.04	0.87	1, 7.98
C_{area}	43.67	<0.001	0.88	9,41	0.36	0.567	0.03	0.9	1, 7.99
N_{area}	14.64	<0.001	0.71	9,41	0.11	0.753	0.01	0.75	1, 8
C:N	34.34	<0.001	0.86	9,41	0.57	0.473	0.05	0.88	1, 7.98
LMA	45.05	<0.001	0.89	9,41	0.3	0.598	0.03	0.91	1, 7.99

Abbreviations and units: area-based respiration at 25°C ($R_{25\text{-area}}$; μmol m^2 s^{-1}); mass-based respiration at 25°C ($R_{25\text{-mass}}$; μmol g^{-1} s^{-1}); per nitrogen-based respiration at 25°C ($R_{25\text{-perN}}$; μmol g^{-1}[N] s^{-1}); leaf mass-based carbon (C_{mass}; mg/g); leaf mass-based nitrogen (N_{mass}; mg$_N$/g); leaf area-based carbon (C_{area}; mg/cm^2); leaf area-based nitrogen (N_{area}; mg$_N$/cm^2) and leaf mass per area (LMA; g/cm^2).

extremes for the Central Highlands of Vietnam. The mean nighttime temperature (MNT) was 13.8°C, whereas the nighttime temperature extremes ranged from a minimum nighttime temperature (NT_{min}) of 4.1°C to a maximum nighttime temperature (NT_{max}) of 20.6°C (Figure 1). Thus, species growing in the Central Highlands are expected to experience temperatures that can vary by 16.5°C which will, in turn, impact their respiratory fluxes and carbon balance. From 2014 to 2016, temperatures ranged by up to 5.9°C from one night to the next. Within a single week, temperatures ranged by up to 9.7°C, and within a single month, temperatures ranged by up to 13.2°C.

Respiration at the NT_{max}, the NT_{min} and the MNT on both an area- and a mass-basis showed similar patterns to $R_{25\text{-area}}$ and $R_{25\text{-mass}}$ (Figure 6; Table 4). Needle-leaved species had significantly higher area-based respiration (R_{area}) than flat-leaved species, but no significant differences were found between leaf morphologies in mass-based respiration (R_{mass}). Likewise, R_{area} and R_{mass} at 4.1, 13.8 and 20.6°C showed similar interspecific patterns to R_{25}, with generally higher R_{area} in species from the Pinaceae than the Podocarpaceae and Taxaceae, and significantly higher R_{mass} in *P. dalatensis* than all other species. We also compared the percent increase from the NT_{min} to the NT_{max} across leaf morphologies and across species (Table 4). No significant differences were found by leaf morphology, likely following the lack of significant differences in the shape of the RT response (*b* and *c*). However, *P. neriifolius* did have a significantly higher % increase in *R* from 4.1°C to 20.6°C than *D. elatum*, *N. nagi* and *P. kesiya*, differences that are reflected in the varying shapes of the species' RT curves.

4 | DISCUSSION

4.1 | Respiratory rates vary between conifers with different leaf morphologies

Shade tolerance has been hypothesized to explain the survival of flat-leaved Podocarpaceae compared to needle-leaved *Pinus* in tropical angiosperm-dominated forests (Bond, 1989; Brodribb & Feild, 2008; Brodribb et al., 2012). We show that *P. krempfii*, the only-known flat-leaved *Pinus*, demonstrates a respiratory flux more similar to coexisting flat-leaved Podocarpaceae than to needle-leaved Pinaceae. This finding aligns with past work showing similarity between *P. krempfii* and flat-leaved Podocarpaceae (Brodribb & Feild, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021). *P. krempfii*'s flattened leaf morphology is enabled by the creation of sclerified tissues for radial water transport to the leaf edge, a method similarly employed in flat-leaved Podocarpaceae (Brodribb, 2011; Brodribb & Feild, 2008; Brodribb & Hill, 1997). Additionally, *P. krempfii* has intermediate rates

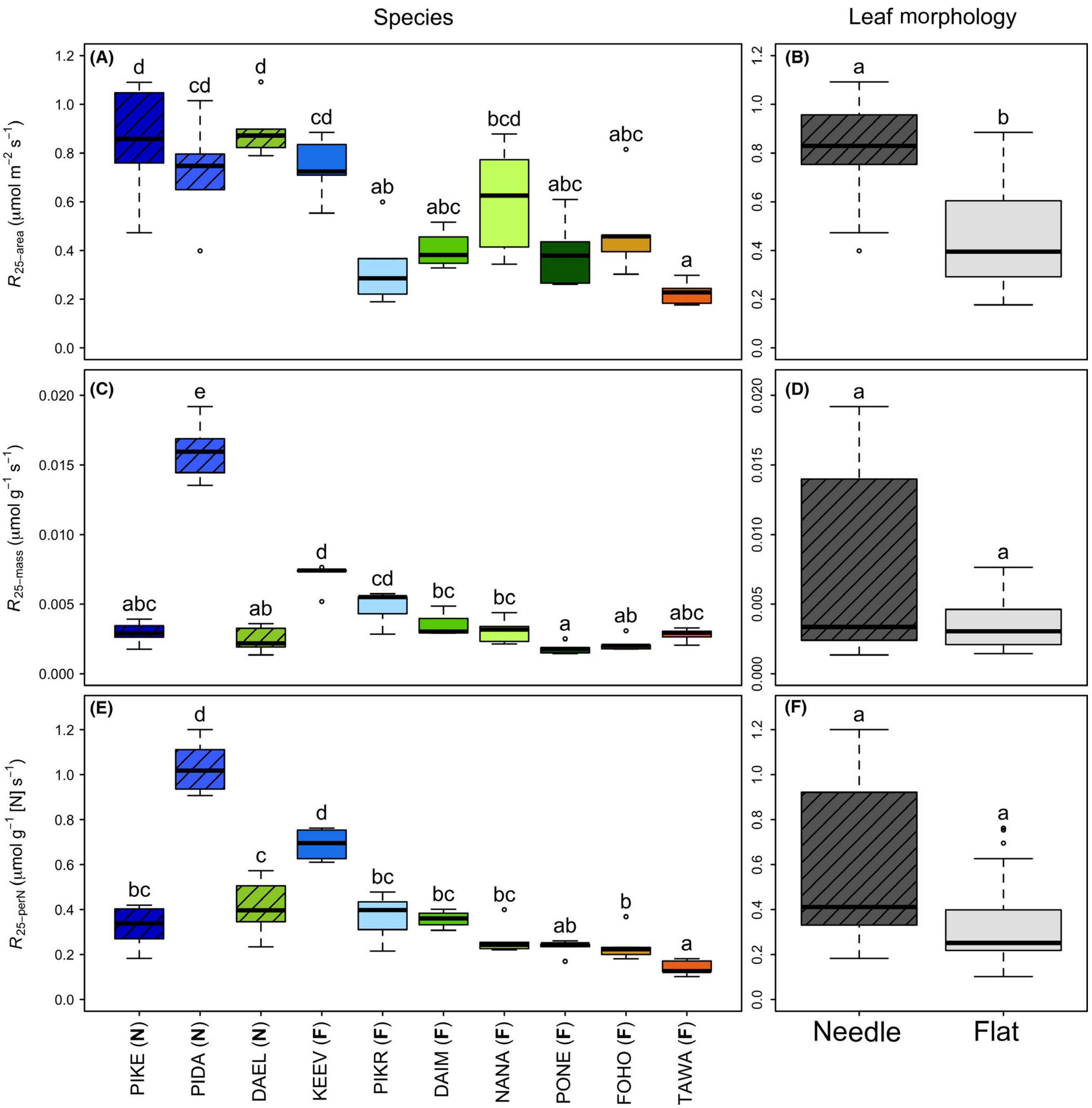

FIGURE 3 Respiration at 25°C (R_{25}) on an area (A, B), mass (C, D) and per nitrogen (E, F) basis for the species and leaf morphologies of the Vietnamese conifers. Species from the Pinaceae in shades of blue, from the Podocarpaceae in shades of green, from the Cupressaceae in yellow and the Taxaceae in orange. Needle-leaved species are cross-hatched and marked by an (N) after each species abbreviation. Flat-leaved species are solid-coloured and marked by an (F) after each species abbreviation. Boxplots represent the median and the first and third quartiles. Whiskers delimit the range for each group, with outliers falling outside 1.5 times the interquartile range marked by points. Significant differences between groups are marked by different letters ($p < 0.05$)

of maximum photosynthesis (Brodribb & Feild, 2008), rubisco carboxylation and photosynthetic electron transport between needle-leaved *Pinus* and flat-leaved Podocarpaceae (Schmiege, Buckley, Stevenson, Cuong, et al., 2021). Not only do our data support past findings in relation to *P. krempfii*, they extend beyond comparisons to *P. krempfii* by showing that flat-leaved conifers have significantly lower $R_{25\text{-area}}$ than needle-leaved conifers.

Differences in $R_{25\text{-area}}$ lend additional support to past findings and the hypothesis that shade tolerance is a survival mechanism of flat-leaved conifers in tropical forests. However, no differences are apparent between leaf morphologies in $R_{25\text{-mass}}$. Although respiration does not depend on light capture as does photosynthesis, it has been found to be a largely area-proportional trait due to the support it provides for the photosynthetic process (Osnas et al., 2013). For

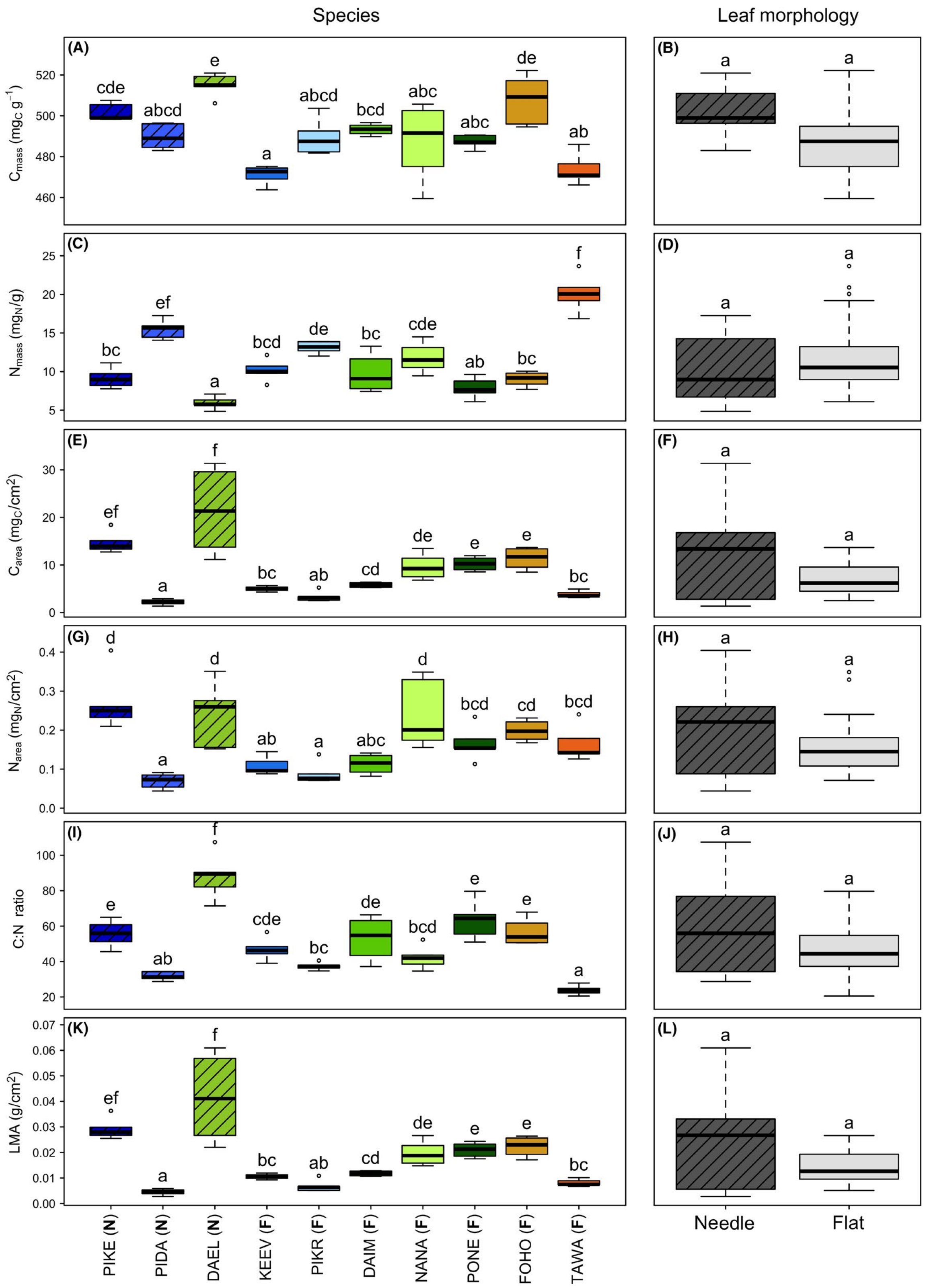

FIGURE 4 Leaf traits for the Vietnamese conifers by species and leaf morphology including mass-based Carbon (C_{mass}; A, B), mass-based Nitrogen (N_{mass}; C, D), leaf area-based carbon (C_{area}; E, F), leaf area-based nitrogen (N_{area}; G, H), the carbon to nitrogen ratio (C:N; I, J) and leaf mass per area (LMA; K, L). Species from the Pinaceae in shades of blue, from the Podocarpaceae in shades of green, from the Cupressaceae in yellow and the Taxaceae in orange. Needle-leaved species are cross-hatched and marked by an (N) after each species abbreviation. Flat-leaved species are solid-coloured and marked by an (F) after each species abbreviation. Boxplots represent the median and the first and third quartiles. Whiskers delimit the range for each group, with outliers falling outside 1.5 times the interquartile range marked by points. Significant differences between groups are marked by different letters ($p < 0.05$)

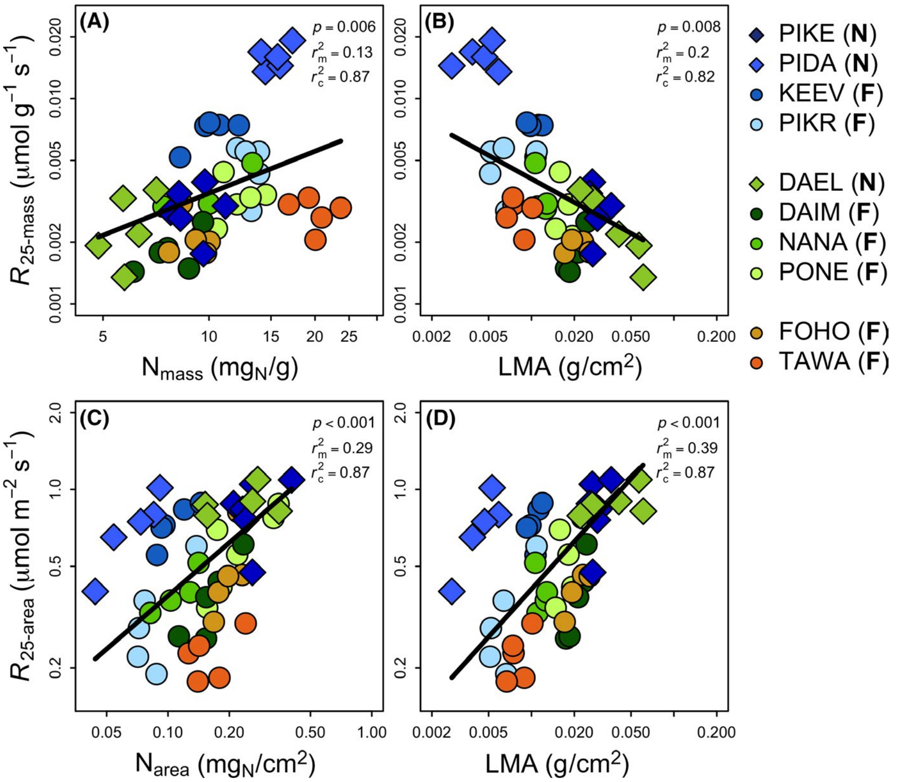

FIGURE 5 Linear mixed-effects relationships between (A) mass-based respiration at 25°C ($R_{25\text{-mass}}$) and mass-based nitrogen (N_{mass}), (B) $R_{25\text{-mass}}$ and leaf mass per area (LMA), (C) area-based respiration ($R_{25\text{-area}}$) and area-based nitrogen (N_{area}), and (D) $R_{25\text{-area}}$ and LMA for the Vietnamese conifers. Species from the Pinaceae are in shades of blue, from the Podocarpaceae in shades of green, from the Cupressaceae in yellow and the Taxaceae in orange. Needle-leaved species are marked by diamonds and (N) after each species abbreviation. Flat-leaved species are marked by circles and (F) after each species abbreviation. Note the log scales in all figures. The relationship was considered significant if $p < 0.05$. Marginal coefficients of determination (r^2_m) and conditional coefficients of determination (r^2_c) are also reported

this reason, and to make more meaningful comparisons to past work focusing on photosynthetic traits, we focus on $R_{25\text{-area}}$ so that we can gain a holistic understanding of leaf carbon balance and shade tolerance in these species. Ultimately, differences between leaf morphologies in $R_{25\text{-area}}$ provide metabolic evidence consistent with a shade-tolerant strategy in flat-leaved conifers, illuminating the physiological underpinnings of broader conifer biogeographical patterns.

Generally, shade-tolerant species have lower respiratory rates than shade-intolerant species (Craine & Reich, 2005; Valladares & Niinemets, 2008; Walters & Reich, 1999). Mechanistically, in shade-tolerant species, limited light availability downregulates photosynthesis and decreases demand for nitrogen-rich photosynthetic proteins and maintenance respiration (Givnish, 1988; Lusk, 2002; Reich et al., 1998; Walters & Reich, 1999). Thus, shade-tolerant species may decrease respiration to maintain a positive carbon balance in environments where photosynthetic carbon gain is limited (Valladares & Niinemets, 2008; Walters & Reich, 1999). Conifers from our study region have a positive relationship between *R* and N, lending support to this explanation. Shade-tolerant species have also been shown to have lower overall plasticity in leaf and physiological traits, leading to lower area-based photosynthetic capacity regardless of whether species are found in high- or low-light conditions (Poorter et al., 2019). Additional studies should certainly examine the intraspecific variation in respiration with irradiance in these unique conifers. However, given the strong correlations between photosynthetic and respiratory fluxes (Reich et al., 1998; Wright et al., 2004), we conclude that lower respiration in flat-leaved species combined with past findings of differences in photosynthetic traits across a large number of needle-leaved *Pinus* and flat-leaved Podocarpaceae (Brodribb & Feild, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021) provide strong consistent evidence for different shade-tolerant strategies across these Vietnamese conifers.

Global analyses have long observed that species fall along a common spectrum of physiological and leaf trait relationships (Wright et al., 2004). Species with fast growth habits and short leaf life spans usually have lower LMA, higher foliar nitrogen content, photosynthesis and respiration than species with tougher, longer-lived leaves (Reich et al., 1998; Wright et al., 2004). Large interspecific variation in LMA and R_{mass} may underlie the lack of detectable significant differences in these and other foliar traits between Vietnamese needle- and flat-leaved conifers, leading to the overall conservation of general trait relationships. In fact, interspecific variability in foliar traits among species growing at similar sites, latitudes or environmental conditions (e.g. the same warmest quarter temperatures; Atkin et al., 2015) is common in the global spectrum of leaf traits (Wright et al., 2004). Analysing the local interspecific variation in basal respiration and associated leaf traits can provide further insights into the local ecology and occurrence of these gymnosperms.

While many of the Vietnamese conifers exist within a similar range of the leaf traits spectrum, *P. dalatensis* had unusually high N_{mass} with extremely low LMA surpassing that of even some of the most fast-growing high-light conifers such as deciduous *Larix* species (Fellner et al., 2016; Gower et al., 1995; Gower & Richards, 1990). The high N_{mass} suggests a larger investment in photosynthetic proteins than in structural defence (Poorter et al., 2009; Reich et al., 1998). Furthermore, *P. dalatensis* is a canopy emergent (Loc et al., 2017), and in a recent Bidoup Nui Ba forest census, very few juveniles were found in the understorey (personal observation). Taken together,

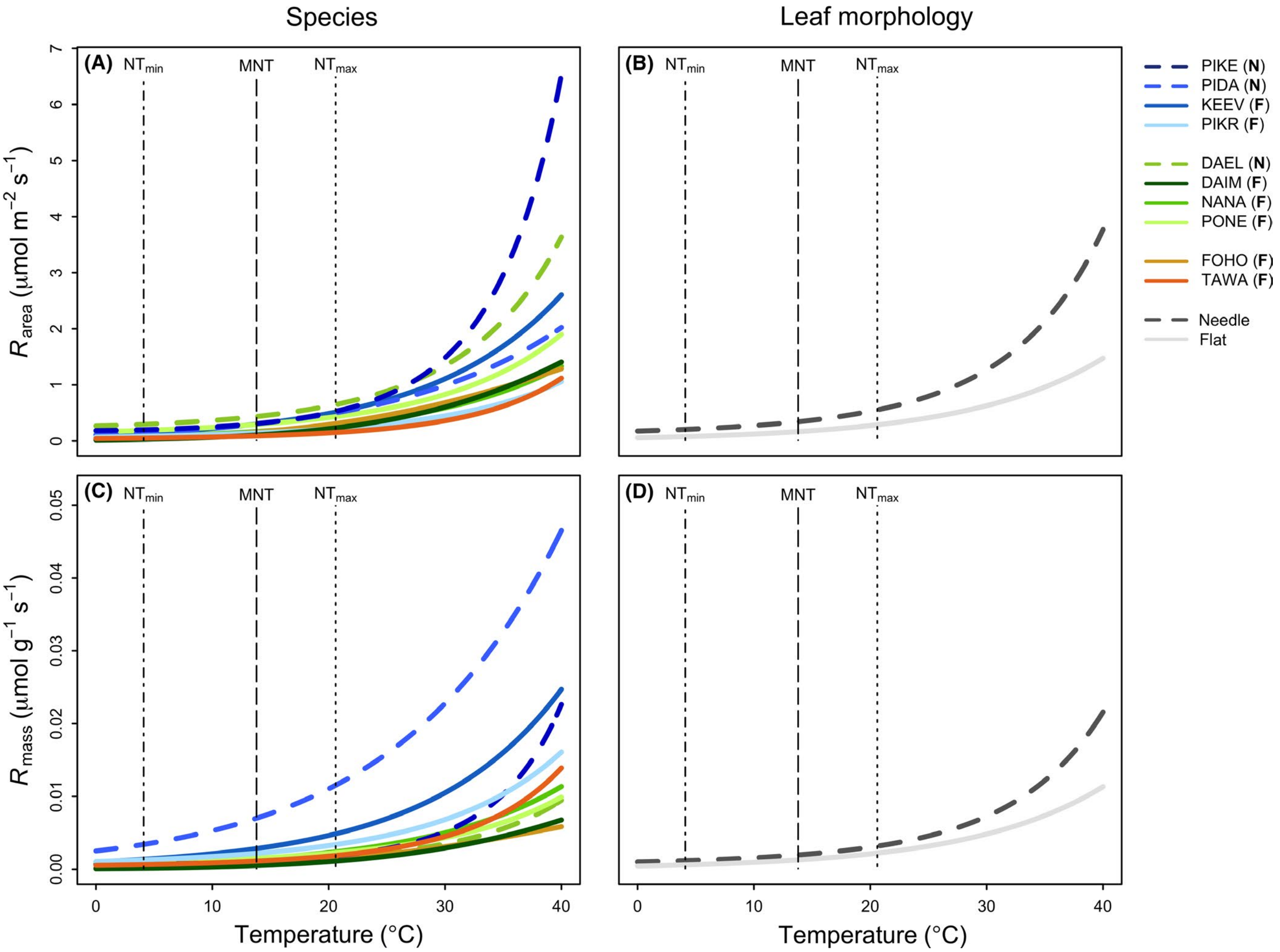

FIGURE 6 Modelled *RT* curves for species and leaf morphologies of the Vietnamese conifers on an area (A, B) and a mass (C, D) basis showing respiratory fluxes at the current mean nighttime temperature (MNT, dashed lines; 13.8°C), the nighttime temperature maximum (NT$_{max}$, dotted lines; 20.6°C) and the nighttime temperature minimum (NT$_{min}$, dot-dashed lines; 4.1°C) calculated from the Giang Ly weather station. Species from the Pinaceae are in shades of blue, from the Podocarpaceae in shades of green, from the Cupressaceae in yellow and the Taxaceae in orange. Needle-leaved species are marked by dashed lines and (N) after each species abbreviation. Flat-leaved species are marked by solid lines and (F) after each species abbreviation

these data suggest that the high N$_{mass}$ and low LMA of *P. dalatensis* facilitate an ecological strategy of rapid vertical growth in forest clearings to become a forest emergent (Ackerly & Bazzaz, 1995; Poorter & Bongers, 2006; Wright et al., 2004).

Pinus kesiya presents an alternate ecological strategy to *P. dalatensis*. Despite high photosynthetic rates (Brodribb & Feild, 2008; Schmiege, Buckley, Stevenson, Cuong, et al., 2021) and high R_{area}, *P. kesiya* does not exhibit high R_{mass} or low LMA. This higher LMA species may invest more in total non-structural carbohydrates or lignin (Poorter et al., 2009), a hypothesis supported by its relatively high foliar C, and previously observed high photosynthetic nitrogen-use efficiency (Schmiege, Buckley, Stevenson, Cuong, et al., 2021). When not under high-light forest-edge conditions, *P. kesiya* may be unable to maintain the high levels of photosynthesis needed for leaves with high construction costs and very short leaf life spans (Kumar Das & Ramakrishnan, 1986), potentially explaining its absence in the forest interior in Vietnam.

Finally, a third strategy is presented by *K. evelyniana*. This species is generally shade intolerant and yet it possesses a flattened but needle-like morphology that is almost intermediate between needle-like Pinaceae and other flat-leaved species. While little is known of the ecology or the physiology of this species, its high $R_{25\text{-}area}$ and high $R_{25\text{-}perN}$ are consistent with other needle-leaved species. Its flattened leaf morphology may increase light capture, and together with its low LMA, lead to its documented success in newly disturbed areas where it is commonly found (Loc et al., 2017). The employment of a flattened leaf morphology in a high-light Pinaceae is extraordinarily uncommon and highlights that potential future research on this species could further illuminate the evolutionary constraints on the biogeographical distribution of predominantly northern hemisphere Pinaceae. Ultimately, the variation in the physiological and morphological traits of these 10 conifers leads to a greater understanding of the multiple mechanisms of conifer survival in this tropical montane forest and the absence of needle-leaved species from the majority of tropical forests.

TABLE 4 Back-transformed mean respiration (±1 *SE*) at the current minimum nighttime temperature (NT_{min}) of 4.1°C, the current mean nighttime temperature (MNT) of 13.8°C ($R_{13.8}$) and current maximum nighttime temperature (NT_{max}) of 20.6°C ($R_{20.6}$) on an area (R_{area}; μmol m^2 s^{-1}) and a mass (R_{mass}; μmol g^{-1} s^{-1}) basis as well as the back-transformed mean % increase in R from 4.1 to 20.6°C for species and leaf morphologies of the conifers of Vietnam. Significant differences between groups are marked by different letters ($p < 0.05$)

Species	$R_{4.1}$	$R_{13.8}$	$R_{20.6}$	% increase $R_{4.1}$ to $R_{20.6}$
R_{area}				
PIKE (N)	0.2 (0.03)^{de}	0.31 (0.04)^{bc}	0.53 (0.06)^{cd}	111 (36)^{a}
PIDA (N)	0.15 (0.03)^{cde}	0.3 (0.04)^{bc}	0.5 (0.07)^{cd}	234 (82)^{ab}
DAEL (N)	0.3 (0.05)^{e}	0.44 (0.06)^{c}	0.65 (0.09)^{d}	100 (35)^{a}
KEEV (F)	0.14 (0.03)^{cde}	0.3 (0.04)^{bc}	0.51 (0.07)^{cd}	257 (90)^{ab}
PIKR (F)	0.08 (0.02)^{bc}	0.14 (0.02)^{a}	0.22 (0.03)^{ab}	161 (57)^{ab}
DAIM (F)	0.08 (0.02)^{bcd}	0.17 (0.02)^{ab}	0.28 (0.04)^{abc}	241 (95)^{ab}
NANA (F)	0.19 (0.03)^{cde}	0.29 (0.03)^{bc}	0.43 (0.05)^{cd}	121 (39)^{a}
PONE (F)	0.03 (0.01)^{a}	0.1 (0.01)^{a}	0.23 (0.03)^{ab}	684 (241)^{b}
FOHO (F)	0.05 (0.01)^{ab}	0.16 (0.02)^{a}	0.31 (0.04)^{bc}	514 (181)^{ab}
TAWA (F)	0.05 (0.01)^{ab}	0.09 (0.01)^{a}	0.15 (0.02)^{a}	184 (65)^{ab}
R_{mass}				
PIKE (N)	0.00069 (0.00011)^{b}	0.00107 (0.00011)^{bc}	0.00183 (0.00019)^{ab}	56 (6)^{a}
PIDA (N)	0.00341 (0.00059)^{c}	0.007 (0.00079)^{f}	0.01153 (0.00128)^{e}	70 (7)^{ab}
DAEL (N)	0.00077 (0.00013)^{b}	0.00113 (0.00013)^{bc}	0.00169 (0.00019)^{ab}	52 (7)^{a}
KEEV (F)	0.00136 (0.00024)^{b}	0.00284 (0.00032)^{e}	0.00486 (0.00054)^{d}	72 (7)^{ab}
PIKR (F)	0.00128 (0.00022)^{b}	0.00218 (0.00025)^{de}	0.00339 (0.00038)^{cd}	62 (7)^{ab}
DAIM (F)	0.0007 (0.00014)^{b}	0.00143 (0.00018)^{cd}	0.0024 (0.0003)^{bc}	71 (7)^{ab}
NANA (F)	0.00097 (0.00016)^{b}	0.00152 (0.00016)^{cd}	0.00226 (0.00023)^{bc}	54 (6)^{a}
PONE (F)	0.00014 (0.00002)^{a}	0.0005 (0.00006)^{a}	0.00111 (0.00012)^{a}	87 (7)^{b}
FOHO (F)	0.00023 (0.00004)^{a}	0.00071 (0.00008)^{ab}	0.00142 (0.00016)^{ab}	83 (7)^{ab}
TAWA (F)	0.00063 (0.00011)^{b}	0.00112 (0.00013)^{bc}	0.00188 (0.00021)^{ab}	64 (7)^{ab}

Leaf morphology	$R_{4.1}$	$R_{13.8}$	$R_{20.6}$	% increase $R_{4.1}$ to $R_{20.6}$
R_{area}				
Needle	0.21 (0.07)^{a}	0.34 (0.08)^{a}	0.56 (0.12)^{a}	137 (47)^{a}
Flat	0.08 (0.02)^{b}	0.16 (0.03)^{b}	0.29 (0.04)^{b}	258 (58)^{a}
R_{mass}				
Needle	0.00122 (0.00061)^{a}	0.00204 (0.00088)^{a}	0.00329 (0.00132)^{a}	59 (7)^{a}
Flat	0.00059 (0.00019)^{a}	0.00127 (0.00036)^{a}	0.00222 (0.00058)^{a}	70 (4)^{a}

4.2 | Convergence and variability in the RT response of conifers with different leaf morphologies

Basal rates of R can vary by environmental conditions, geographical range, PFT and leaf traits (Patterson et al., 2018; Reich et al., 1998; Slot et al., 2014). The significantly higher a_{area} of needle-leaved species compared to flat-leaved species agrees with the trending curve offset differences found between needle-leaved evergreen and broad-leaved tropical PFTs (Heskel et al., 2016). As all our species coexist in the same forest, potentially confounding effects of site growth temperature are removed, further emphasizing fundamental metabolic differences among PFTs. Higher basal respiration in needle-leaved conifers may indicate that needle-leaved foliage is more energetically costly, providing a possible metabolic explanation for why pines are so uncommon in the tropics. High basal respiration, combined with what we know of the role of photosynthetic rates and leaf shapes in shade tolerance strategies, lends further support that needle-leaved pines may be unsuccessful in low-light environments. The continued presence of several natural pines in the Central Highlands is unusual; however, the balance between photosynthesis and respiration can often explain species' growth abilities and dominance (Heskel et al., 2013), and all Vietnamese conifers showed extremely high carbon gain efficiency at the seedling stage (Schmiege, Buckley, Stevenson, Cuong, et al., 2021). Additional research on the whole-plant R in seedlings may further illuminate survival strategies of needle-leaved conifer seedlings of these unusual Vietnamese pines (Baltzer & Thomas, 2007).

In contrast to the observed differences in basal respiration, there were no significant differences in flat- and needle-leaved species in the shape of the *RT* response, consistent with the past work of Heskel et al. (2016). More recent work using macromolecular rate theory even suggests that such a convergence might be mechanistically explained by a common temperature response of respiratory enzymes across all plants (Liang et al., 2018). While we show no significant differences in *b* and *c* between needle- and flat-leaved species, it is interesting that the majority of these conifers have a positive *c* parameter that is in contrast with the primarily negative values of Heskel et al. (2016). The ecological significance of this subtle difference in the shape of the *RT* curve is currently unknown; however, it is interesting that other studies have also found positive *c* in conifers when compared to broad-leaved deciduous angiosperms (Patterson et al., 2018). A positive *c* means that respiration will approach infinity at very high and very low temperatures, so extreme caution should be used in applying this equation beyond the 10–40°C range over which the equation was originally fit. Despite the similarity in the shape of the *RT* response across conifer leaf morphologies, species-specific differences in the shape of the *RT* response are apparent and highlight that some species may experience larger % increases in *R* with normal fluctuations in nighttime temperatures. Nightly fluctuations of up to 5.9°C and weekly fluctuations of up to 9.7°C as seen in 2014–2016 may markedly increase respiratory fluxes in some species such as *P. neriifolius* compared to others such as *D. elatum*, *N. nagi* and *P. kesiya*. The short timeframes over which these fluctuations occur may preclude acclimation of respiration to these new temperatures (Zhu et al., 2021), raising the important question of how expected future increases in temperature (Ho et al., 2011) as well as increases in the frequency of extreme events (Diffenbaugh & Scherer, 2011; Ho et al., 2011) might affect the carbon balance of these unique conifer species. Future studies examining the magnitude of the long-term acclimation of *R* to *T* as well as the photosynthetic temperature response of conifers and tropical montane species from across a breadth of biogeographical regions are urgently needed (but see Mujawamariya et al., 2021). Such studies, in addition to our own study of the short-term *RT* response, will provide a clearer understanding of the effects of future temperature regimes on the continued presence of the gymnosperms in this forest, and illuminate the effects of rising temperatures on tropical montane forest composition and carbon storage.

5 | CONCLUSIONS

We examined the respiratory temperature response of conifer species with contrasting leaf morphologies that coexist in a tropical montane forest in the Central Highlands of Vietnam. The high conifer diversity provides a unique opportunity to assess the role of metabolic physiology and morphology in determining the dominance of broad-leaved conifers over needle-leaved conifers in tropical forests. We found that flat-leaved conifers had lower area-based basal respiration and lower $R_{25\text{-area}}$, providing metabolic support for shade tolerance as a driver of flat-leaved Podocarpaceae success and needle-leaved Pinaceae absence across tropical forests. Furthermore, interspecific differences in the *RT* response of these conifers highlight the need for future studies to examine, in more detail, the impacts of rising temperatures and increases in extreme temperature events on the growth and survival of these regionally important conifer species.

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AUTHORS' CONTRIBUTIONS

S.C.S. and K.L.G. designed the study; S.C.S., K.L.G., B.M.B., T.Q.C. and L.C.N. collected the data; S.C.S. analysed the data; S.C.S., K.L.G., D.W.S., B.M.B. and M.A.H. wrote the manuscript. All authors contributed to drafts and approved the final version for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.b5mkkwhcz (Schmiege, Buckley, Stevenson, Heskel, et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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