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Loïc GILLEROT

Dries LANDUYT

Rachel OH

Winston T. L. CHOW *Singapore Management University*, winstonchow@smu.edu.sg

et al

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RESEARCH ARTICLE

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Forest structure and composition alleviate human thermal stress

Loïc Gillerot^{1,2} | Dries Landuyt¹ | Rachel Oh^{3,4} | Winston Chow⁵ | Daniela Haluza⁶ | Quentin Ponette⁷ | Hervé Jactel⁸ | Helge Bruelheide⁹ | Bogdan Jaroszewicz¹⁰ | Michael Scherer-Lorenzen¹¹ | Pieter De Frenne¹ | Bart Muys² | Kris Verheyen¹

¹Forest & Nature Lab, Department of Environment, Ghent University, Melle-Gontrode, Belgium
²Division of Forest, Nature and Landscape, Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium
³German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
⁴Department of Ecosystem Services, Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany
⁵School of Social Sciences, Singapore Management University, Singapore, Singapore
⁶Department of Environmental Health, Center for Public Health, Medical University of Vienna, Vienna, Austria
⁷Earth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium
⁸Biogeco, INRAE, University of Bordeaux, Cestas, France
⁹Institute of Biology, Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany
¹⁰Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Warsaw, Poland

¹¹Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany

Correspondence

Loïc Gillerot, Forest & Nature Lab, Department of Environment, Ghent University, Geraardbergsesteenweg 267, Gontrode 9090, Belgium. Email: loic.gillerot@ugent.be

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Abstract

Current climate change aggravates human health hazards posed by heat stress. Forests can locally mitigate this by acting as strong thermal buffers, yet potential mediation by forest ecological characteristics remains underexplored. We report over 14 months of hourly microclimate data from 131 forest plots across four European countries and compare these to open-field controls using physiologically equivalent temperature (PET) to reflect human thermal perception. Forests slightly tempered cold extremes, but the strongest buffering occurred under very hot conditions (PET > 35°C), where forests reduced strong to extreme heat stress day occurrence by 84.1%. Mature forests cooled the microclimate by 12.1 to 14.5°C PET under, respectively, strong and extreme heat stress conditions. Even young plantations reduced those conditions by 10°C PET. Forest structure strongly modulated the buffering capacity, which was enhanced by increasing stand density, canopy height and canopy closure. Tree species composition had a more modest yet significant influence: that is, strongly shadecasting, small-leaved evergreen species amplified cooling. Tree diversity had little direct influences, though indirect effects through stand structure remain possible. Forests in general, both young and mature, are thus strong thermal stress reducers, but their cooling potential can be even further amplified, given targeted (urban) forest management that considers these new insights.

Pieter De Frenne, Bart Muys and Kris Verheyen should be considered joint senior authors.

KEYWORDS

Dr. Forest, forest microclimate, heat mitigation, heat stress, nature-based solution, physiologically equivalent temperature, thermal comfort

1 | INTRODUCTION

Temperature extremes have been unequivocally linked to excess human morbidity and mortality (Anderson & Bell, 2009; Baccini et al., 2008; Ye et al., 2012), with heatwaves being the deadliest weather-related cause of mortality in Europe (Forzieri et al., 2017) and the United States (Luber & McGeehin, 2008). Potential non-fatal health outcomes resulting from physiological heat stress are cardiovascular, renal or respiratory complications and heat strokes (Ye et al., 2012), but also include adverse impacts on mental state, energy levels and sleep quality (Tawatsupa et al., 2012). Large heatwavecaused excess mortality events are already commonplace globally (Mora et al., 2017), with an estimated cumulative death toll record of 345,000 within the 65+ age group in 2019 (Romanello et al., 2021). The global health burden will intensify significantly in the coming decades (Basarin et al., 2020; Mora et al., 2017; Romanello et al., 2021) as heatwaves will increase in frequency and severity as a result of global warming (IPCC, 2021). In Europe, a 50-fold increase in mortality is projected as 27%-63% of the population will be exposed to heatwaves in the period 2071-2100 under business-as-usual conditions (Forzieri et al., 2017). This trend is echoed at the global scale, where about 48% of the world's population is estimated to be subjected to lethal heat thresholds for at least 20 days per year by 2100 under the most optimistic climate change scenarios (Mora et al., 2017). Dangerously hot conditions are thus virtually unavoidable in the future (Mora et al., 2017; Romanello et al., 2021), with markedly increased risks for inhabitants of currently warm climates (Forzieri et al., 2017; Xu et al., 2020).

Heat mitigation strategies range from national to local measures. Among others, these include developing national heat health warning systems, installing air conditioning and water vaporizers, increasing urban infrastructure's albedo, and deploying shade-casting tissues above highly visited and heat-prone streets (Basarin et al., 2020; De' Donato et al., 2015; Romanello et al., 2021; Taleghani, 2018). Increasing the vegetation cover is a nature-based solution of particular interest, because it supports a plethora of additional physical and psychological health benefits such as improving air quality, reducing stress and promoting physical activity (Marselle et al., 2019; van den Bosch & Ode Sang, 2017). Vegetation generally improves thermal comfort by evapotranspiration and shading, and, in urban contexts, also by obstructing dark impervious surfaces from accumulating heat (Bowler et al., 2010; Taleghani, 2018). Urban cooling vegetation can take the form of grasslands, green roofs and green walls, each of which significantly improve thermal comfort (Bowler et al., 2010; Santamouris et al., 2020; Taleghani, 2018). However, because human heat perception is highly sensitive to solar radiation (Höppe, 1999; Taleghani et al., 2015; Thorsson et al., 2007), trees and

forests usually generate greater thermal comfort by providing additional cooling through shading (Norton et al., 2015; Taleghani, 2018). A meta-analysis found that parks have an average daytime cooling effect of 0.94°C, with an increased tree cover further improving cooling (Bowler et al., 2010). This cooling effect sharply increases under hot conditions. For every 1% increase in tree cover, a decrease of 0.14°C in air temperature was predicted for the hot and arid city of Phoenix, USA (Middel et al., 2015), and another study found a decrease of 1.6–2.5°C in air temperature maxima under dense canopies in Hong Kong, China (Kong et al., 2017). Increasing the city's tree cover by 10% could even compensate heat stress caused by moderate climate change scenarios (Middel et al., 2015; Zölch et al., 2016).

Forest microclimates have also been studied extensively to assess the biodiversity impacts of climate change (De Frenne et al., 2021). Recent large-scale studies reported a cooling of air temperature maxima by 2.1°C in European forests (Zellweger et al., 2019) and 4.1°C in forests globally (De Frenne et al., 2019). Here as well, thermal buffering effects became increasingly apparent the warmer it got outside of the forests (De Frenne et al., 2019), exemplified by a mean forest cooling effect of 5.2°C documented during a 11-day heatwave in Switzerland (Renaud & Rebetez, 2009). This buffering capacity can be substantially modulated by forest structural attributes such as basal area, canopy closure and canopy height (Greiser et al., 2018: Jucker et al., 2018: von Arx et al., 2012). Fewer studies also found buffer-enhancing effects of the tree species composition (Renaud & Rebetez, 2009), and even fewer suggested a positive species diversity effect mediated by a more complete canopy packing (Ehbrecht et al., 2017; Zhang et al., 2022).

Yet, these aforementioned forest buffering effects can only partially be translated into thermal stress reductions, because human temperature perception is strongly influenced by physical factors beyond air temperature alone. Thermal perception and concomitant physiological stress are best quantified using indices based on the body's energy balance that take into account air temperature and humidity, mean radiant temperature and wind speed (Jendritzky et al., 2012; Johansson et al., 2014), such as the physiologically equivalent temperature (PET-not to be confused with "potential evapotranspiration" which has the same acronym) (Mayer & Höppe, 1987). Studies at the thermal comfort and urban forestry nexus using such indices often highlight even stronger contrasts between grey and green settings. A striking example comes from Zabol, Iran, where urban vegetation reduced the air temperature by 1°C, but by 7°C in PET (Davtalab et al., 2020). Thermal buffering by forests from a human health perspective must therefore imperatively be quantified using relevant indicators.

Here we use an interdisciplinary toolbox drawing from urban planning, biometeorology and ecology to investigate the thermal buffering capacity of forests to improve human thermal comfort and reducing heat hazards to humans. We quantified the forest buffering capacity using PET, as it is by far the most commonly applied index (Potchter et al., 2018), it is valid under a large range of thermal conditions and it has an easily interpretable unit (°C) (Matzarakis et al., 1999). We addressed a key knowledge gap by quantifying the influence of forest ecological characteristics including tree diversity, stand structure and tree species composition. To enhance generality, we measured the forest microclimate in eight regions and 131 forest plots distributed across Europe. Plots covered both young plantations and mature (semi-)natural forests, including a total of 17 tree species represented as both monocultures and three-species mixtures. This study was conducted under the ERA-net BiodivERsA project "Dr. Forest," which researches the link between forest biodiversity and human health.

2 MATERIALS AND METHODS

2.1 Study sites and sampling design

We established a total of eight study sites across four European countries (Belgium, France, Germany and Poland), covering a climatic gradient from oceanic to sub-continental. Five were young forest plantations from the TreeDivNet network (hereafter "young plantations") (treedivnet.ugent.be) (Paguette et al., 2018; Verheyen et al., 2016). The three remaining sites comprised mature (semi-) natural forest stands (hereafter "mature forests"), two of which are part of the Exploratory Platform of the FunDivEUROPE project (Baeten et al., 2013) while the third site belongs to the TREEWEB network (De Groote et al., 2017). All sites were specifically designed to study biodiversity effects on ecosystem functioning. The young plantations benefit from controlling for factors such as edaphic conditions, stand size and the spatial arrangement of tree species. Complementary to those assets, the mature forest stands are more representative of natural conditions while still minimizing confounding environmental factors (e.g., soil, topography and disturbances).

At each site, we selected a range of 12-20 plots with one or three tree species, and added two control plots. This amounted to a total of 147 plots, of which 131 were forest plots and 16 were controls. Species in mixed stands were always present as monospecific stands and both stand types were present in equal numbers per site. Control plots were defined as nearby (<5 km) open fields, with no vegetation higher than the sensors (i.e., 1.1 m high) and at least 30 m away from the nearest trees and forest edge. This was to ensure that the influence of tall and woody vegetation on thermal conditions was kept to a minimum. See Table S1 for site and plot characteristics, including tree species compositions.

2.2 **Microclimatic measures**

Where possible, microclimate stations were installed in the center of each forest plot. In young plantations, however, the center of Global Change Biology –WILEY 3

three-species plots often did not coincide with a point of intersection of the three tree species because species were planted in blocks of multiple individuals. To ensure an approximately equal influence of each species, sensors were placed at the intersection of plantation blocks where the three species were directly side-by-side, as close to the plot center as possible. As for mature forest plots, the sensors were always mounted at an equidistance of three evenly large trees (diameter at breast height>20cm), either pertaining to the same species in case of the monospecific stands or to the three different species for mixed stands. Sensors were mounted on a wooden pole at 1.1 m height, representing the average center of gravity of a standing adult human (ISO, 1998; Johansson et al., 2014).

The microclimate stations recorded data continuously from August/September 2020 to October/November 2021. We therefore had a total of 147 complete time series spanning 14-16 months, with some exceptions due to logger malfunctioning or damage by animals and humans-representing 0.3% of the data. More details are found in the dedicated section "Missing data and substitutions" in the Methods S1. We measured four bioclimatic variables shown to influence human thermal comfort: air temperature, relative humidity, mean radiant temperature (T_{mrt}) and wind speed (Johansson et al., 2014; Matzarakis et al., 1999; Mayer & Höppe, 1987). The microclimate stations were programmed to record air temperature and relative humidity every hour, and the $\mathrm{T}_{\mathrm{mrt}}$ and wind speed every 30 min. In June 2021, we increased the data logging frequency to 15 min for all variables to improve temporal resolution during summer. Air temperature, relative humidity and T_{mrt} were measured at the plot level using Lascar EL-USB-2 and EL-USB-TC sensors, while wind speed was measured at the site level using a cup anemometer coupled to a Lascar EL-USB-5 data logger. The four microclimatic parameters (air temperature, relative humidity, T_{mrt} and wind speed) enable the calculation of the PET (Mayer & Höppe, 1987), which is the most commonly used thermal comfort index (Potchter et al., 2018). Details on microclimatic measures, data manipulations and PET calculations are found in Methods S1. A simplified explanation of the concepts behind PET is provided in Box 1.

2.3 Forest buffering effect calculation

The forest buffering effect was calculated as the offset in PET values between thermal conditions inside and outside the forests (i.e., control plots). First, daily statistics were calculated per plot: daily PET maxima and minima (respectively PET_{\max} and PET_{\min}) and the daily means (PET mean). For control plots, resulting PET values were averaged per site and retained as a proxy variable representing the macroclimate (i.e., PET_{max/min} control), because forest buffering was expected to depend on thermal conditions outside the forest. Based on calculations of the difference between daily PET values in both controls per site, the mean discrepancy between controls was 0.19°C, with a standard deviation of 0.54°C. This indicates existing but small differences in thermal conditions between control plots of the same site. Next, the offsets were calculated as forest PET values

BOX 1 Physiologically equivalent temperature

In lay terms, PET is equivalent to the air temperature of a standardized room that would generate the same temperature perception as one would experience in the complex outdoor environment being measured (Höppe, 1999; Mayer & Höppe, 1987). For example, a person standing outside in the sun while the air temperature is 30°C could easily experience a PET of 43°C because of the high solar radiation, meaning that this person feels the same heat as in the standardized room with air temperature 43°C. Conversely, on a cold and windy winter day, PET values can be easily 10°C lower than air temperatures (Höppe, 1999).

PET is based on a physiological model that calculates heat exchanges between the environment and a human body, considering the body's core, skin and clothing temperatures. Some examples of considered heat flows include loss of latent heat following transpiration and the gain of heat due to internal heat production caused by metabolic activity (Höppe, 1999).

minus PET_{max/min} control. The resulting data are daily offset values for the 131 forest plots (PET_{max/min} offset), with negative values representing a forest cooling effect, and vice versa.

2.4 Forest structure, composition and diversity measures

All measures were done within circular subplots of 7 m (young plantations) or 9 m (mature forests), with microclimate stations representing their center. Forest structure was represented by three main variables related to stand density, canopy height and canopy openness. Stand density was quantified using basal area, which represents the cross-sectional area of tree stems at breast height per hectare. Canopy height was estimated by averaging the heights of each dominant tree in three diverging directions (0°, 120° and 240°C relative to the microclimate station, with $0^\circ =$ north). Canopy openness was measured using a spherical densiometer where readings were converted to the percentage of open sky seen from below the canopy (Baudry et al., 2014). Canopy openness was also assessed using hemispherical photography, which showed high congruity with densiometer measures.

Species compositional effects were calculated using visual estimation of species-specific canopy covers based on the vertical projection of tree crowns (Zellweger et al., 2019). Using these species-specific estimations as weights, we calculated the average leaf area based on values obtained from the TRY plant trait database (Kattge et al., 2020) and the average shade-casting ability (SCA) of tree species within the subplot. The SCA represents a species' ability

to cast shade, ranging from 1 (very low shade, e.g., Betula pendula) to 5 (very deep shade, e.g., Fagus sylvatica) (Verheyen et al., 2012). Still using species-specific canopy covers, we determined the proportion of deciduous trees to investigate whether thermal buffering would be reduced in the leaf-off season.

At last, tree species diversity was represented by the Shannon-Wiener index, based on the relative contributions of each species in terms of basal area (sensu Nickmans, 2019). Initially, 17 'focal' tree species were included, but our sampling strategy added 12 more tree and shrub species (>1 m tall) to the dataset. Refer to Methods S1 for extended methodological details and measured variables that were not retained in final models.

2.5 Data analyses

In the current study, we assess to which extent the forest buffering capacity (i.e., PET_{max/min} offset) is influenced by forest structure (i.e., dominant canopy height, basal area and canopy openness), composition (i.e., SCA, proportion of deciduous trees and leaf area) and diversity (i.e., Shannon diversity based on basal area). Because forest ecological traits are interrelated and may have both direct and indirect effects (e.g., a higher basal area may directly lead to improved buffering, but also indirectly through reduced canopy openness), we applied structural equation modeling (SEM) to our dataset. The SEM model selection followed the guidelines proposed by Grace et al. (2012). The analyses were conducted for two periods: when deciduous trees were bearing leaves (May-November) and when they were leafless (December-April). Note that the leaf area variable was omitted for the leaf-off analyses, but we kept the canopy openness variable because leafless (deciduous) branches may still influence the microclimate (Sjöman et al., 2016), albeit much less. Using the final SEM structure based on PET_{max} offset (prioritized because of the strongest relevance for human health), we repeated the analyses for PET_{\min} offset (and PET_{\max} offset) to keep models comparable. Analyses aimed to unveil the relative effects of forest variables, not to reach the simplest model, which is why our final SEMs include non-significant variables. We used piecewise SEM to enable the use of linear mixed models (LMMs) involving temporal autocorrelation (Lefcheck, 2016). SEM models were built in R v4.1.1 (R Core Team, 2013) using the package piecewiseSEM v2.1.0 (Lefcheck, 2016). See Methods S1 for details on the LMMs integrated in the SEM and for the calculation of total effects sizes, and Dataset S1 for the complete dataset.

RESULTS 3

Pooled forest buffering effects 3.1

Forest stands had a consistent thermal buffering effect across sites, highly dependent on macroclimatic conditions (i.e., PET conditions outside the forest) (Figure 1). Daily PET maxima (PET_{max}) were little



FIGURE 1 Thermal buffering effect of forests on daily physiologically equivalent temperature (PET) maxima (a) and PET minima (b), expressed in offsets (respectively, PET_{max} offset and PET_{min} offset). Offsets equal the PET inside the forest minus the PET outside the forest (macroclimate), with negative values representing a forest cooling effect and vice versa. Offsets are given for each of the eight studied sites in function of thermal stress at the macroclimatic level partitioned according to physiological stress categories defined by Matzarakis et al. (1999). The light grey violin plots in the background represent the total offset distribution regardless of macroclimate conditions. PET measures were conducted from the end of the summer 2020 until the end of autumn 2021. See Figure S2 for results using PET_{mean}.

reduced by forests under macroclimatic conditions that represent slight to extreme cold stress. When the macroclimate engendered no thermal stress (18°C < PET < 23°C), forests showed pronounced cooling effects: -3.64 ± 3.51 °C PET (mean ± SD) reduction in young plantations and -3.08 ± 2.96 °C PET in mature forests. Under conditions corresponding to strong (35°C < PET <41°C) and extreme (PET >41°C) heat stress, forest cooled the thermal environment with, respectively, -10.03 ± 4.59 °C PET and -9.97 ± 5.19 °C PET for young plantations, and respectively, -12.13 ± 2.88 °C PET and -14.53 ± 2.87 °C PET for mature forests. This is the equivalent of

reducing physiological thermal stress by two to three heat stress categories, resulting in an 84.1% reduction in strong to extreme heat stress days in terms of PET_{max} in the forest (see Table S2 and Figure 1 for results per heat stress category).

Conversely, daily PET minima (PET_{min}) were only slightly warmer in the forest and moderately dependent on the macroclimate. When macroclimatic minima corresponded to no thermal stress, the forest warming effect was $+0.78\pm0.84^{\circ}$ C for young plantations and $+1.08\pm1.08^{\circ}$ C for mature forests. Under very cold conditions (PET <4°C), the warming effect rose to $+2.44\pm2.02^{\circ}$ C for young ⁶ WILEY Global Change Biology

plantations and $\pm 4.07 \pm 2.45$ °C for mature forests. Based on PET_{min}, the forest reduced the occurrence of strong to extreme cold days by 17.9% (Figure S1). Analysis results using PET_{mean} are found in Figure S3.

3.2 | Forest structure, composition and diversity effects on thermal buffering

Forest structure (assessed using basal area, canopy height and canopy openness as proxies) had a strong positive influence on the forest's buffering capacity, followed by variables related to species composition and identity (Figures 2 and 3). Tree diversity consistently had the weakest influence. Macroclimatic conditions (PET_{max/min} control) were key in controlling the magnitude of the

buffering capacity, but they also strongly interacted with multiple forest structure variables. This interaction indicates that forest structure effects increase when macroclimatic conditions increasingly deviate from average conditions.

Based on the pseudo- R^2 (Nakagawa & Schielzeth, 2013), the PET_{max} model for the leaf-on season explained the largest proportion of variation in forest buffering capacities (marginal $R^2 = 0.68$ and conditional $R^2 = 0.73$). In all cases, the leaf-on season models always explained more variation compared to their leaf-off counterparts (leaf-off being relevant for deciduous trees, while evergreen species remain leafed) (Figure S3), suggesting that the forest affects the microclimate more strongly when its canopy is fully leafed.

Basal area was a strong predictor of canopy openness (Figure 2) and also strongly reduced PET_{max} offsets in interaction with the macroclimate (PET_{max} control) during the leaf-on season (Figure 3).



FIGURE 2 Structural equation models for (a) forest buffering effects on physiologically equivalent temperature maxima (PET_{max}) during the leaf-on season and (b) on minima (PET_{min}) during the leaf-off season. PET_{max} control and PET_{min} control represent macroclimatic conditions and have important interactions with forest variables, represented by yellow arrows and hexagons. Generally, the stronger the deviation from average PET values, the stronger the forest trait effects become. Effect sizes are standardized by range. Marginal (R^2_{m}) and conditional (R^2_{c}) R^2 values of the fitted linear mixed-effect models are shown below each response variable. H'_{BA,Scaled}, Shannon diversity index based on basal area; H_{avg}, dominant canopy height; BA, basal area; SCA, shade-casting ability; LA, leaf area; DeciProp, proportion of deciduous trees; CO_{Densio (log}), canopy openness densiometer (log-transformed); PET_{max/min} control, maximum/minimum PET value reached on under open-field control conditions; PET_{max/min} offset, difference in maximum/minimum PET value between forest and open-field conditions. See Table S3 for an overview of variables and Figure S3 for results of the other tested models. The upper half of each SEM includes N = 131 observations, corresponding to the number of forest plots. The lower part includes N = 55,797 observations, corresponding to the total number of day-level measures over all plots. Significance levels are denoted as follows: *p < .05; **p < .01; ***p < .001.



FIGURE 3 Total estimated effect sizes of the predictor variables determining (a) physiologically equivalent temperature maxima (PET_{max}) and (b) minima (PET_{min}) buffering, based on direct and indirect effects plus relevant interactions with PET_{max/min} control. The more negative, the stronger the relative cooling effect, and vice versa. Error bars represent the standard deviation based on Monte Carlo simulations. Coefficients were scaled prior to total effect estimation to assure their comparability. H'BA, Scaled = Shannon diversity index based on basal area, BA = basal area, H_{avg} = dominant canopy height, CO_{Densio} = canopy openness densiometer, SCA = shade-casting ability, DeciProp = proportion of deciduous trees, LA = leaf area. More details on the calculations are provided in Methods S1.

Species composition

This relative cooling effect was significant over all models-when considering the interaction-except for PET_{\min} buffering in the leaf-on season. Stand height had a modest direct cooling effect on PET_{max} offset during the leaf-on season, which was again exacerbated by the macroclimate. The lower the canopy openness, the stronger the cooling of PET_{max} , and this was strongly exacerbated by the macroclimate. Canopy openness itself was mainly determined by basal area, leaf area and SCA.

Forest structure

Forest diversity

Concerning the species composition variables, a slight but significant relative warming effect of PET_{max} (and relative cooling of PET_{min}) was observed for an increasing proportion of deciduous trees, indicating that buffering effects are weakly magnified in stands with a high proportion of evergreen trees. Following this logic, the PET_{max}

cooling effect of evergreen trees was stronger in the season where deciduous species were leafless. Both SCA and leaf area had marked total effects on thermal buffering which are comparable in magnitude but differed in directionality. While an increasing SCA enhanced microclimate relative cooling, an increased leaf area led to relative warming. Their direct effects on buffering were moderate, but their large and significant influence on canopy openness led to a strong indirect effect.

Tree diversity had no significant impacts on microclimatic variation, except for $\mathsf{PET}_{\mathrm{mean}}$ offsetting during the leaf-off season in interaction with the macroclimate (p = .01). Other direct, indirect and interacting pathways were insignificant across the models, and this is reflected in the small aggregated effect sizes (Figure 3).

4 | DISCUSSION

4.1 | Pooled forest buffering effects

We found forests across eight regions in Europe to have a considerable cooling capacity on the thermal environment. When openfield conditions corresponded to slight heat stress or warmer, forest were cooler by 6.1°C up to 14.5°C PET and thereby strongly reduced heat stress. Even though not directly comparable, this well exceeds magnitudes based on air temperature alone found by large-scale ecological surveys reporting a forest cooling effect of 2.1°C on average in European forests and 4.1°C globally (De Frenne et al., 2019; Zellweger et al., 2019), using a similar study design. This is likely due to their focus on air temperature and relative humidity, which is adopted in most ecological studies (Bramer et al., 2018), whereas accurate estimations of human thermal perception also need to consider wind speed and, crucially, mean radiant temperature (Chen & Matzarakis, 2018; Johansson et al., 2014; Mayer & Höppe, 1987). In fact, the mean radiant temperature, together with air temperature, is often cited as the most important factor for thermal perception (Nikolopoulou & Lykoudis, 2006; Taleghani et al., 2015; Thorsson et al., 2007), which is also taken into account by the physiological model underlying our PET results (Chen & Matzarakis, 2018; Höppe, 1999). The strong reductions in heat stress we observed are thus partly explained by the important roles of trees and forests in reducing the mean radiant temperature specifically, which they do directly by shading people from direct solar radiation and indirectly by shading below-canopy surfaces that would otherwise generate shortwave reflection and longwave emission (Norton et al., 2015; Shashua-Bar et al., 2011; Taleghani, 2018; Zölch et al., 2016). Furthermore, that also explains why cooling by forests will be most effective on sunny days and, expressed in spatial terms, in those regions with abundant solar radiation. To a lesser extent, forests will also reduce heat stress through evaporative cooling (Rahman et al., 2020; Taleghani, 2018), which has the advantage of cooling the air temperature within the shade but also outside the forest (Kong et al., 2017).

In contrast with ecological studies, urban planning and human biometeorology studies frequently use thermal indicators suited for human perception, but most often focus on single trees or small tree clusters instead of forests. This nevertheless yields impressive examples, with an average reduction in PET of 4.7–5.3 °C observed under single street trees in Melbourne, Australia (Sanusi et al., 2017), or the reductions of 0.84-17.5°C PET for individual trees and 0.3-15.7°C for tree clusters in Campinas, Brazil (de Abreu-Harbich et al., 2015). However, these cooling effects are usually expressed relative to impervious urban surfaces, which, in concert with the urban heat island effect, heat up much more than open grasslands which were our control conditions. The microclimatic contrasts we observed would therefore undoubtedly be even higher if our controls had represented typical urban settings like an asphalted street or a paved city square. In contrast, our usage of a white, unventilated PVC shield may have led to an overestimation of the air temperature under

warm and sunny conditions in the open control plots relative to temperatures measured with thermocouples or in Stevenson shields (Maclean et al., 2021). Overestimated air temperatures might have magnified obtained PET cooling values, although such an overestimation would be partially compensated by reducing the difference between air and globe temperatures, which decreases the calculated mean radiant temperature and ultimately PET (see the Methods S1, section "Potential for cooling overestimation").

We found a consistent but modest warming effect on daily PET minima. This is the result of accumulating radiation and reemitting it more slowly than open field conditions, created by reduced air mixing due to wind blocking (Davies-Colley & Payne, 2000; De Frenne et al., 2021; Hardwick et al., 2015). Substantiating this idea, we found forests to reduce wind speed with a factor 4.53 on average over the eight sites (range = 1.92-6.95). The forest warming effect is also evidenced by the aforementioned large-scale ecological studies, which reported minimum air temperature warming of up to 1.1°C on average, ranging up to 6°C (De Frenne et al., 2019; Zellweger et al., 2019). These magnitudes are more comparable to our findings relative to our very large maxima reductions. These diverging results highlight the strong influence of solar radiation on thermal comfort during daytime and the strongly reduced transmittance in forests. The warming of PET minima, however, is in strong contrast with studies in cities which demonstrate that the presence of urban trees reduces nighttime temperatures because vegetated surfaces store much less radiant energy compared to urban surfaces (Bowler et al., 2010; Harlan et al., 2006).

4.2 | Forest structure, composition and diversity effects on thermal buffering

Our results indicate that variation in buffering capacities is driven by forest ecological characteristics, especially stand structure and species composition. Ecological studies have observed air temperature extremes to be tempered under denser forests and canopies because of reduced incoming and outgoing radiation, higher evapotranspiration and lower air mixing (Chen et al., 1999; Hardwick et al., 2015; von Arx et al., 2012; Zellweger et al., 2019). More specifically, air temperature buffering was shown to be increased by basal area and canopy closure (Greiser et al., 2018), leaf area index (Hardwick et al., 2015; von Arx et al., 2013), biomass and structural complexity (Frey et al., 2016) and below-canopy vegetation density (Kovács et al., 2017). Similarly aligned with our results, canopy height was previously found important (Frey et al., 2016; Jucker et al., 2018), and could be compared to the thickness of an insulating cover. We revealed that these conclusions appear transposable to human thermal comfort.

Human-centered studies, in contrast to ecological studies, typically focus on tree-level structural characteristics. Results are therefore only partly comparable to our findings, but show analogous patterns. For example, not forest structure, but tree structure expressed as crown size, shape and density, trunk architecture and tree height was demonstrated to drive cooling capacities (de Abreu-Harbich et al., 2015; Kong et al., 2017; Rahman et al., 2020; Wang et al., 2019). Our strong canopy effects mirror another set of findings pinpointing the dominant effects of leaf and plant area index (Sanusi et al., 2017; Shahidan et al., 2010), resulting from reducing the transmittivity of solar radiation by thick branching, twigs and leaves (Shahidan et al., 2010). High branch area indices were even found to improve thermal comfort (Sjöman et al., 2016), which could partially explain why we still found strong canopy effects during the leaf-off season.

Compositional effects played a secondary yet significant role in further improving thermal comfort, with strongly shade-casting evergreen species with small leaves having greater buffering capacity. Corroborating our results, beech-composed stands (Fagus sylvatica), a wide-spread Central European species that is a strong shade caster (Verheyen et al., 2012), were particularly efficient at cooling the air temperature during the 2003 heatwave in Switzerland (Renaud & Rebetez, 2009). However, in contrast with our findings of stronger cooling by evergreen species, the strongest summer and daytime cooling effect was observed in mixed deciduous and deciduous forests (Renaud et al., 2011; Renaud & Rebetez, 2009), though a global meta-analysis did not detect such a tree species effect (De Frenne et al., 2019). Broadleaved trees and non-pine conifers were found to have double the buffering effect compared to pines during daytime (von Arx et al., 2012). Deciduous species have been argued to be superior in terms of human thermal comfort at the annual scale in temperate regions, given that high transmissivity can actually be beneficial during colder, leafless months (Konarska et al., 2014; Sjöman et al., 2016). We found a weak indication for the opposing outcome, possibly because the dense evergreen trees we studied might reduce wind speed and simultaneously enhance heat accumulation in lower air layers. Forest stands composed of small-leaved species also seemed to enhance cooling. Literature hints at similar patterns, with an urban planning study finding a small-leaved tree species to provide the strongest cooling out of 12 species (de Abreu-Harbich et al., 2015), and a recent meta-analysis pointing to needle leaves as the superior shape (Rahman et al., 2020).

Tree species diversity consistently seemed to be of little influence, although an indirect effect was anticipated based on theory and recent findings (Zhang et al., 2022). Species diversity is expected to be linked to structural complexity because of higher potential for spatial complementarity in aboveground biomass leading to a more complete canopy space filling (Pretzsch, 2014; Pretzsch et al., 2016), driven by increased vertical stratification and especially crown plasticity of trees grown in mixtures (Jucker et al., 2015) and ultimately improving microclimatic buffering (Ehbrecht et al., 2017; Zhang et al., 2022). Our SEM analyses do not indicate a strong coupling of tree diversity and canopy closure. Diversity effects may be manifested more subtly through pathways not captured by our momentary measures, such as by underlying long-term increases in tree biomass due to improved spatiotemporal partitioning of belowground and aboveground resources (Ammer, 2019; Scherer-Lorenzen, 2014), or by changes in water use and transpiration

(Grossiord, 2020). Additionally, the weak direct diversity effects we observed might partially result from the hardly stratified canopies in plantations, which may substantially affect canopy space filling in further development stages (Zhang et al., 2022). Indeed, indications of a diversity effect exist, such as recent findings of a significantly amplified air temperature buffering in 50% of sampled young forest plantation mixtures (Zhang et al., 2022), and a 0.2°C increase in land surface temperature cooling capacity for every 0.1 increase in Shannon-Wiener diversity of tree species in summer (Wang et al., 2021).

4.3 Management implications and conclusions

Our results are directly relevant for the well-being and health of people visiting forests for recreational purposes. A limitation of this study is that this direct relevance is relatively restricted beyond recreation because the majority of people do not permanently live in forests. Severe health implications due to thermal stress are also disproportionally more frequent in vulnerable groups of the populations (young children, the elderly, people with low incomes and those with pre-existing medical conditions) (Harlan et al., 2006; Romanello et al., 2021; Ye et al., 2012), which are less prone to seek cooling in the forest when conditions become hazardous. For these reasons. nearly all studies on thermal stress reduction by vegetation focus on urban environments, where a globally quickly increasing urban population (United Nations, Department of Economic and Social Affairs, Population Division, 2019) spends a large proportion of their time and where heat stress is more stringent due to the urban heat island effect (Oke, 1973; Rahman et al., 2020). Even though our results are based on non-urban forests compared to open-field conditions, they are also relevant to urbanized settings given the consistency and magnitude of observed cooling effects, that are expected to be even more pronounced when compared to typical urban infrastructure which traps much more heat than our open fields. Furthermore, forest cooling effects are not only perceptible inside the forest, but also up to hundreds of meters outside forested parks (Bowler et al., 2010; Wang et al., 2021), which further indicates that increasing urban forest cover could foster safer living conditions for many, even for those not living directly within or next to a forest stand. One priority should thus be to improve accessibility to cool forest microclimates, small urban forest stands could, for example, be fairly distributed over populous areas and especially in the vicinity of vulnerable age groups and communities (Harlan et al., 2006; McDonald et al., 2021). Aligning with that idea, the recently proposed 3-30-300 rule in recommends that every urbanite should be able to see three trees from their home, that every neighborhood should have a canopy cover of at least 30% and that no citizen would live further than 300 m of a greenspace (≥0.5 ha) (Konijnendijk, 2021).

Another priority for mitigating anticipated increases in heat stress events is to direct non-urban and urban forest management toward forest characteristics that enhance thermal buffering. Our results indicate that heat reduction will be strongest in a

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mature forest with a high basal area, tall trees and a dense canopy. Moreover, it should be (co-)composed of small-leaved evergreen species that cast a deep shade and bear a large total leaf area for a given ground surface area. The tree species diversity seems of limited direct importance for PET buffering. These are all variables that can be targeted by forest management, even in most urban forests. According to the Forest and Agriculture Organization of the United Nations (FAO), urban forests are "networks or systems comprising all woodlands, groups of trees, and individual trees located in urban and peri-urban areas; they include, therefore, forests, street trees, trees in parks and gardens, and trees in derelict corners" (FAO, 2016). Since our analyses include numerous young plantations with surfaces below 0.5 ha and with canopy openness well over 50%, our results can apply even to small urban forest stands that are defined by FAO as "pocket parks and gardens with trees (<0.5 ha)," though not to "trees on streets or in public squares" which refer to individual trees and which we did not study. Auspiciously, even plantations, only a decade after planting, exhibited a huge potential to improve thermal comfort, particularly under hot conditions.

Preserving forests and safeguarding existing canopies may thus locally diminish heat stress risks to human health and partially counter the additional burden posed by current climate change. Similarly, forest canopies also mitigate climate change impacts on biodiversity as many forest species partially depend on its stable, cooler microclimate (Chen et al., 1999; Zellweger et al., 2020). Our findings suggest that promoting tree planting and afforestation, and encouraging access to recreational forest areas, is likely to lead to huge thermal stress reductions while providing a multitude of additional human health benefits (Karjalainen et al., 2010; Marselle et al., 2019; Wolf et al., 2020).

AUTHOR CONTRIBUTIONS

Loïc Gillerot: conceptualization; formal analysis; investigation; writing-original draft preparation. Dries Landuyt: formal analysis; writing-review & editing, supervision. Rachel Oh: writing-review & editing. Winston Chow: writing-review & editing. Daniela Haluza: funding acquisition; writing-review & editing. Quentin Ponette: funding acquisition; project administration; writing-review & editing. Hervé Jactel: funding acquisition; project administration; writing-review & editing. Helge Bruelheide: funding acquisition; project administration. Bogdan Jaroszewicz: funding acquisition; project administration; writing-review & editing. Michael Scherer-Lorenzen: funding acquisition; project administration; writingreview & editing. Pieter De Frenne: methodology; writing-review & editing; supervision. Bart Muys: conceptualization; funding acquisition; project administration; writing-review & editing; supervision. Kris Verheyen: conceptualization; funding acquisition; project administration; writing-review & editing; supervision.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The complete dataset, including both forest ecological characteristics and biometeorological variables is, available in Figshare at 10.6084/m9.figshare.19494818.

ORCID

Loïc Gillerot [®] https://orcid.org/0000-0002-0699-4478 Dries Landuyt [®] https://orcid.org/0000-0003-2716-7727 Winston Chow [®] https://orcid.org/0000-0003-1819-597X Daniela Haluza [®] https://orcid.org/0000-0001-5619-2863 Quentin Ponette [®] https://orcid.org/0000-0002-2726-7392 Hervé Jactel [®] https://orcid.org/0000-0002-8106-5310 Helge Bruelheide [®] https://orcid.org/0000-0003-3135-0356 Bogdan Jaroszewicz [®] https://orcid.org/0000-0002-2042-8245 Michael Scherer-Lorenzen [®] https://orcid.

Pieter De Frenne D https://orcid.org/0000-0002-8613-0943

Bart Muys https://orcid.org/0000-0002-8813-0943 Kris Verheyen https://orcid.org/0000-0002-2067-9108

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