

Peatland evaporation across hemispheres: contrasting controls and sensitivity to climate warming driven by plant functional types

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Abstract. Peatlands store disproportionately large amounts of carbon per unit area, a function that is dependent on maintaining high and stable water tables. Climate change is likely to negatively impact carbon storage in peatlands, in part due to increases in vapour pressure deficit (VPD) driving higher evaporation (E) rates. However, the response of E to increasing VPD depends on the dominant vegetation type within peatlands. In this study, we used multiple years of eddy covariance (EC) measurements to compare E regimes at two peatlands with contrasting vegetation types – Kopuatai bog in Aotearoa New Zealand, dominated by the vascular wire rush *Empodisma robustum*, and Mer Bleue bog in Canada, a ‘typical’ shrub and moss-dominated Northern Hemisphere peatland. We examined seasonal variability in E and equilibrium E (E_{eq}), energy balance partitioning, and the response of E , evaporative fraction (EF), and canopy conductance (g_c) to VPD. Mean annual E was 45% lower than mean annual E_{eq} at Kopuatai, but only 16% lower at Mer Bleue, demonstrating much greater limitations on E at Kopuatai. In addition, the mean midday (10:00–14:30) dry canopy Bowen ratio (β) at Kopuatai was 2.0, compared to 0.8 at Mer Bleue; therefore, the sensible heat flux (H) dominated over the latent heat flux (LE) at Kopuatai, and vice versa at Mer Bleue. The responses of E , EF, and g_c to increasing VPD at Kopuatai demonstrated stronger limitations on evaporative water loss for VPD > 0.7 kPa compared to Mer Bleue. The observed limitations at Kopuatai were attributed to strong stomatal control by *E. robustum* due to the rapid decrease in g_c with increasing VPD, however surface E could also be limited by its dense standing litter. At Mer Bleue, however, E was only weakly limited at VPD > 2 kPa, likely due to weak stomatal control over transpiration by the sparse shrub canopy and relatively large surface E from *Sphagnum* carpets. As such, the results of this study suggest that *E. robustum* drives a greater “hydrological resistance” to increasing VPD than the vegetation at Mer Bleue, leading to greater water retention at Kopuatai. This may enable greater resilience of the carbon sink function at Kopuatai to climatic warming and drying than at Mer Bleue.

1 Introduction

Global peatlands have accumulated carbon (C) stocks of at least 500 Pg over thousands of years, resulting in a net cooling effect on the climate (Yu et al., 2010; Frohling and Roulet, 2007). This C stock is estimated to make up a third of global soil C (based on a median estimate of 1460.5 Pg), despite only occupying ~3% of Earth's land surface area (Scharlemann et al., 2014; Xu et al., 2018). Carbon accumulation as peat occurs in undisturbed peatlands when the rate of organic matter deposition exceeds decomposition, due to limitations imposed on decomposition by waterlogged conditions and the presence of decay-resistant plant litter (Joosten and Clarke, 2002; Holden, 2005). Therefore, long-term C sequestration in peatlands depends on maintaining a high and stable water table (Kim et al., 2021; Ma et al., 2022).

Evaporation (E)¹ is an important indirect influence on peat accumulation, as it reduces available water and contributes to water table drawdown. Evaporation consists of three main components – transpiration, surface E (either from water, soil, or non-vascular plant surfaces), and interception loss from vegetation surfaces – and is influenced by a number of meteorological (solar radiation, vapour pressure deficit (VPD)) and surface factors (vegetation type and water table depth (WTD); Takagi et al., 1999; Shimoyama et al., 2003; Wu et al., 2010). In bog ecosystems, where precipitation is the sole water input (Holden, 2005), conservation of water is particularly important; this occurs through limitations imposed on E by bog vegetation (Campbell and Williamson, 1997), as well as limitations on lateral and vertical drainage by low hydraulic conductivity of the highly decomposed peat soils (Fraser et al., 2001). As such, vegetation type is often a major factor regulating water loss from bogs (Lafleur and Roulet, 1992; Takagi et al., 1999; Admiral et al., 2006).

The response of E to increasing atmospheric demand, i.e., increasing VPD, is of particular interest, as climate change-related warming has been predicted to elevate VPD (Ficklin and Novick, 2017; Fang et al., 2022). Plant responses to changing VPD are known to affect transpiration rates and CO₂ uptake (Grossiord et al., 2020). With increasing VPD, contrasting E responses have been observed across different vegetation types (Takagi et al., 1999; Admiral et al., 2006; Massman et al., 2019) and ecosystems (Helbig et al., 2020). For example, using eddy covariance (EC) data from 95 boreal peatland and forest sites, Helbig et al. (2020) demonstrated that E rates were elevated by increasing VPD in both ecosystem types, however E rates were 30% higher in boreal peatlands than in boreal forests at high VPD. This suggests that the stability of peatland hydrological regimes and C stores may be at risk under future changes to the climate.

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Kopuatai bog is a warm-temperate, ombrotrophic peatland on Te Ika-a-Māui/North Island of Aotearoa New Zealand. The vegetation at Kopuatai is dominated by the vascular plant *Empodisma robustum*, which has been implicated in severely restricting E (Campbell and Williamson, 1997). The hypothesised mechanisms for this are stomatal control of transpiration

¹ 'Evaporation' refers to the bulk flux of water vapour from land, including transpiration. We do not use the term 'evapotranspiration', as both evaporation and transpiration involve the transformation of water from a liquid to a vapour (Miralles et al., 2020).

and limitation of surface E due to restricted water vapour diffusion from the substrate through the dense standing litter layer
60 (Campbell and Williamson, 1997; Thompson et al., 1999). Carbon uptake at Kopuatai is greater than in analogous Northern
Hemisphere peatlands, and exhibits resilience to drought (i.e., high annual net ecosystem C balance despite drought disturbance
in summer; Goodrich et al., 2017). This could be a result of the year-round growing conditions (Campbell et al., 2014), in
contrast to the temperature-limited growing season lengths in Northern Hemisphere peatlands which constrain C uptake
(Roehm and Roulet, 2003; Lafleur et al., 2001; Helfter et al., 2015). However, high C uptake rates and drought resilience could
65 also be indirectly attributed to the extremely low E , which maximises available water and maintains a high and stable water
table. Therefore, the *resilience* of C uptake at Kopuatai could be due to *resistance* of the hydrological regime to environmental
stressors through limitations on E (based on resistance and resilience definitions from Nimmo et al., 2015). As such, E
limitation could be a very important self-regulation mechanism in this peatland ecosystem type.

70 Like Kopuatai, many peatlands have formed in warm climates; however, the majority of the global peatland area occurs in
boreal regions of the Northern Hemisphere (Vitt, 2006). One such peatland is Mer Bleue bog in Canada, a shrub and *Sphagnum*
moss-dominated bog ecosystem located in a cool continental climate zone (Moore et al., 2002). As one of the most studied
Northern Hemisphere peatlands, Mer Bleue has a long record of E measurements and knowledge of E processes. Daily E rates
at Mer Bleue are comparable to many other Northern Hemisphere peatlands, and have been shown to be affected by water
75 table depth (E is limited by deep water tables; Lafleur et al., 2005), available energy (drives increases in E), and VPD (the
effect of which varies depending on the partitioning of E between vascular and non-vascular sources; Admiral et al., 2006).
The average net annual C uptake at Mer Bleue is much lower than at Kopuatai, primarily due to net C losses during the winter
period and a shorter growing season (Roulet et al., 2007; Goodrich et al., 2017).

80 Knowledge of E at Kopuatai bog is limited to the results of two short-term studies (Campbell and Williamson, 1997; Thompson
et al., 1999), so our understanding of the variability and mechanisms of E restriction by *E. robustum* is incomplete. In addition,
it is not yet known how these limitations on E may affect the response of the ecosystem at Kopuatai to climate warming,
including its C sink status. Therefore, the aim of this study is to compare the E regime at Kopuatai to that of Mer Bleue, as an
example of a 'typical' Northern Hemisphere peatland, to better understand the relative sensitivity of these systems to
85 hydrological change under continued climate warming. Compared with previous studies, our study utilises multi-annual
datasets at each site, thereby analysing E characteristics over a wide range of climate and weather conditions. The objectives
of this study are to (1) compare seasonal variability in actual E and equilibrium E (E_{eq}) at Kopuatai and Mer Bleue, (2)
investigate energy balance partitioning and (3) examine the responses of E , evaporative fraction (EF), and canopy conductance
(g_c) to VPD at each site. Our hypothesis is that differences in seasonal E limitations, energy balance partitioning, and responses
90 of E to VPD, such that more water is conserved at Kopuatai relative to Mer Bleue, can be attributed to differences in vegetation.
If this hypothesis is correct, it is possible that the water-conserving traits of *E. robustum* will enable greater resistance of the

hydrological regime, and hence greater resilience of the C stores, to climate warming compared to typical Northern Hemisphere peatlands.

2 Methodology

95 2.1 Site descriptions

2.1.1 Kopuatai bog

Kopuatai bog is a 96 km² ombrotrophic peatland located in a warm-temperate oceanic climate in the Waikato region of Aotearoa New Zealand (37.388° S, 175.554° E). Kopuatai is Aotearoa's largest undisturbed bog, a remnant of formerly widespread and diverse lowland wetlands; these ecosystems have been reduced to 10% of their previous extent due to
100 widespread drainage, primarily for agriculture (McGlone, 2009; Dymond et al., 2021). Peat at Kopuatai has accumulated over the last 11,700 years at an average rate of 0.9 mm year⁻¹, with a maximum depth of 14 m (Newnham et al., 1995; Shearer, 1997). Probing at the research site showed a peat depth of 11 m.

The dominant peat-forming vegetation at Kopuatai is *E. robustum* (Wagstaff and Clarkson, 2012), a vascular, evergreen jointed
105 rush-like plant that is part of the family Restionaceae (known as 'restiads'; Wagstaff and Clarkson, 2012). At the field site, *E. robustum* has a mean leaf area index (LAI) of 1.32 (Goodrich et al., 2015) and a mean canopy height of 0.48 m. *E. robustum* forms a dense, negatively geotropic surface root mat approximately 50 mm thick which can hold up to 15 times its dry weight in water (Campbell, 1964; Agnew et al., 1993; Clarkson et al., 2009). In addition, *E. robustum* has a dense standing litter layer (litter biomass = 0.92 kg m⁻², where total canopy biomass = 1.80 kg m⁻²), which can restrict water vapour diffusion from the
110 peat surface by limiting turbulent transport (Campbell and Williamson, 1997; Keyte Beattie, 2014). However, *E. robustum* can also restrict water loss via transpiration through strong stomatal control (Campbell and Williamson, 1997). The roots of *E. robustum* are the main material from which peat is formed, however live mosses and decayed canopy litter are also bound by these roots and contribute to peat formation (Campbell, 1964; Agnew et al., 1993). Other vegetation types found at this site include sedges (*Machaerina* spp. and *Schoenus brevifolius*), isolated shrubs of *Leptospermum scoparium* (manuka) and
115 *Epacris pauciflora*, as well as small patches of *Sporadanthus ferrugineus*, another restiad plant.

2.1.2 Mer Bleue bog

Mer Bleue bog is a 28 km² ombrotrophic peatland (45.411° N, -75.481° E) located near Ottawa, Canada, in a cool continental climate. Mer Bleue has many features in common with boreal peatlands but is located near the southern limit of the boreal climate zone (Hember et al., 2005). This peatland was initiated 8,400 years ago as a fen, transitioning into a bog around
120 7,100–6,800 years ago (Roulet et al., 2007). At the research site, the bog is characterised by hummock-hollow

microtopography, and has peat depths of 5–6 m (Lafleur et al., 2005). The hummock height at Mer Bleue is 0.25 m, with a 70% cover of hummocks. The dominant vegetation consists of evergreen ericaceous and deciduous shrubs (e.g., *Chamaedaphne calyculata*, *Rhododendron groenlandicum*, *Kalmia angustifolium*, *Kalmia polifolia*, *Vaccinium myrtilloides*), with *Sphagnum* moss species as the dominant ground cover, including *S. capillifolium*, *S. papillosum*, and *S. magellanicum* (Bubier et al., 2006). The average shrub canopy height is 0.18 m (range = 0.10–0.30 m; Bubier et al., 2006); shrub vegetation makes up 61% of the total biomass on average, while *Sphagnum capitula* make up 30% (Moore et al., 2002). The total biomass ranges between 0.147 and 1.011 kg m⁻², while the LAI of dominant vascular species is 1.3 on average (Moore et al., 2002; Bubier et al., 2006).

2.2 Data collection and processing

130 2.2.1 Data collection

Flux tower and ancillary data have been collected at both sites for many years – in this study, data covering 1 January 2012 to 31 December 2022 at Kopuatai (11 years) and 1 January 1999 to 31 December 2018 at Mer Bleue (20 years) were used. At each site, 30-minute fluxes of latent heat (*LE*), sensible heat (*H*), soil heat (*G*) and net radiation (*R_n*), along with 30-minute data on environmental and weather variables, including air temperature (*T_{air}*), vapour pressure deficit (VPD), precipitation (*P*), and water table depth (WTD; measured relative to the hummock surface at Mer Bleue, while the Kopuatai peat surface lacks hummocks and hollows), were collected. Latent and sensible heat fluxes were measured using the eddy covariance (EC) technique (Burba, 2022). The EC system at Kopuatai is an open path system (Appendix A) situated at 4.25 m height, with uninterrupted fetch greater than 500 m in all directions (research site is shown in Fig. 1a). At Mer Bleue, a closed path EC system is situated at 3.0 m height, with a fetch greater than 500 m in all directions except south, where it is 200–300 m (Fig. 140 1b).

Following collection, flux data were quality-controlled and gap-filled. For gap-filling of *LE* and *H* at Kopuatai, separate daytime and night-time neural network models used drivers of *R_n*, *T_{air}*, VPD, and modelled canopy wetness state (detailed below); further details on data processing, quality control, and gap-filling are provided in Goodrich et al. (2017). At Mer Bleue, gap-filling of *LE* was carried out by developing a linear relationship between available energy (*R_a*) and *LE* for summer, and calculating a multiplier to adjust the estimated *LE* to observed *LE* over a moving window period (the window width was 100 half-hours with available data moved in increments of 20 half-hours). *R_a* was calculated as *R_n* minus the rate of change in *G* (calculated using peat temperature profiles) and energy storage terms (*J*). Gap-filled sensible heat fluxes were then calculated as the difference between *R_a* and *LE*. For both sites, gap-filled flux data were used for seasonal to annual *E* totals, while other analyses only used filtered measurements. 150

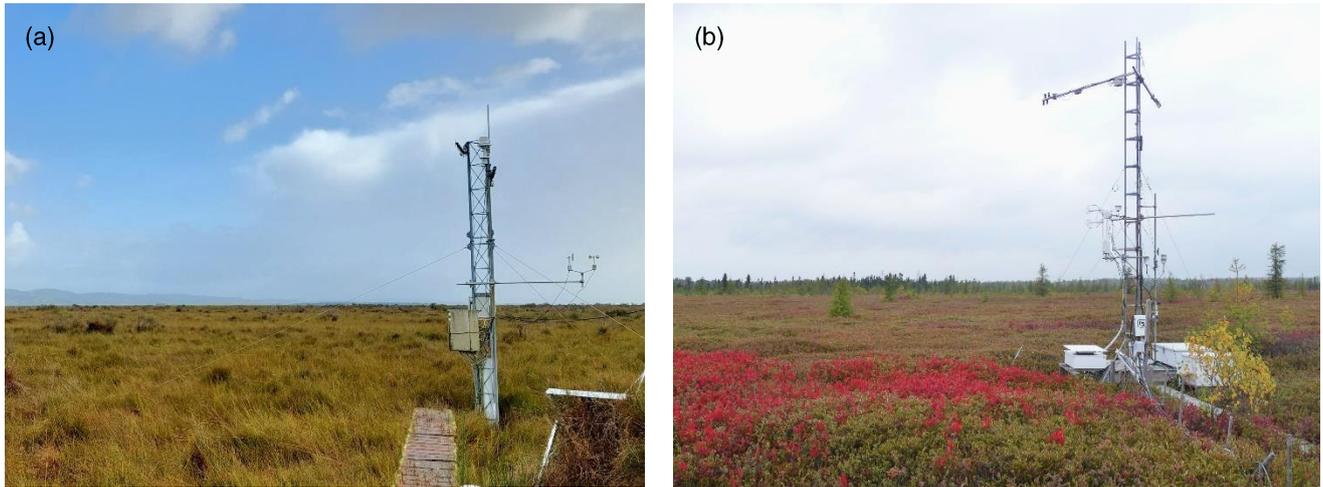


Figure 1. Images of the two sites including eddy covariance towers at (a) Kopuatai and (b) Mer Bleue.

2.2.2 Equilibrium evaporation

To provide a reference E rate at each site, the equilibrium evaporation (E_{eq}) was calculated using 24-hour mean data:

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$$E_{\text{eq}} = \frac{s(R_n - G)}{L_v(s + \gamma)} \quad (1)$$

where s is the slope of the saturation vapour pressure versus air temperature curve, L_v is the latent heat of vaporisation (dependent on T_{air}), and γ is the psychrometric constant ($0.066 \text{ kPa } ^\circ\text{C}^{-1}$). G was assumed to be 0 W m^{-2} due to the use of 24-hour mean data.

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The ratio E/E_{eq} , i.e. the Priestley–Taylor α , was then calculated in order to be able to compare E regimes at the two sites despite differing climates. Gap-filled LE data were converted to $E = LE/L_v$ for this analysis.

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Equilibrium E was selected as a measure of potential E as it provides a more conservative estimate compared to other methods, such as the Penman equation (Granger, 1989). In addition, E_{eq} is less dependent on energy partitioning compared to Penman open water E (Thompson et al., 1999). As explained by Thompson et al. (1999), due to the high ratio of sensible to latent heat flux (i.e., a high Bowen ratio, β) at Kopuatai, VPD is potentially larger than it would be above an extensive water surface in the same region, driving Penman open water E to an unrealistic level. Due to the lack of a VPD term in the E_{eq} equation, this effect is mitigated.

170 2.2.3 Energy balance partitioning and VPD analysis

The analysis of energy balance partitioning and the relationships of E , EF , and g_c with VPD involved the use of non-gap-filled E , R_n , LE , H , VPD, and wind speed data, pre-filtered through quality control protocols. Further filtering was then carried out to obtain data for growing season months (May–October at Mer Bleue and September–May at Kopuatai). In addition, all 30-minute data from both sites were filtered to select only “middle-of-day” (MoD) conditions (10:00–14:30 local standard
175 time), with an additional filter of $R_n \geq 200 \text{ W m}^{-2}$ applied to the VPD analysis. These 30-minute data were also filtered by dry or wet canopy conditions, which were identified using an antecedent precipitation index (API; Appendix B); an $API \leq 0.2$ signifies a dry canopy, while $API \geq 1$ indicates fully wet canopy conditions. These filtered 30-minute data were then used to calculate MoD means of all variables. Days with less than five (50%) acceptable 30-minute data points for all variables were removed to ensure representative MoD means. Overall, this filtering resulted in 58% and 66% of MoD dry canopy 30-minute
180 data being rejected for Kopuatai and Mer Bleue, respectively. However, for wet canopy conditions, 90% (Kopuatai) and 92% (Mer Bleue) of MoD 30-minute data were rejected. For the following analyses, 95% confidence intervals were calculated for MoD means as the standard error multiplied by 1.96.

To analyse energy balance partitioning, filtered growing season MoD mean LE and H data were binned by R_n (bin width =
185 50 W m^{-2}) for each site, taking the mean value of each bin. This was calculated separately for dry and wet canopy conditions. Seasonal energy balance partitioning was also investigated by calculating monthly means of MoD dry canopy LE , H , and R_n ; however, no other filters were applied to the data for this particular component of the analysis.

To demonstrate the relationship between evaporative water loss and VPD, filtered dry canopy growing season MoD means of
190 E , EF , and g_c were binned by VPD (0.1 kPa intervals), following Helbig et al. (2020), taking the mean of each bin for all variables. Evaporative fraction was used to assess the change in energy balance partitioning into LE with increasing VPD and was calculated as:

$$EF = \frac{\overline{LE}}{\overline{LE} + \overline{H}} \quad (2)$$

195 The denominator $LE + H$ was used rather than R_n to prevent incomplete energy balance closure (Appendix C) from affecting our results. In addition, β was calculated as:

$$\beta = \frac{H}{LE} \quad (3)$$

Finally, g_c was calculated following Campbell and Williamson (1997):

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$$\frac{1}{g_c} = \frac{(1 + \beta) \rho c_p \text{VPD}}{\gamma R_n} + \frac{r_a s \beta}{\gamma} - r_a \quad (4)$$

where ρ is air density (1.2 kg m^{-3}), c_p is the specific heat of air ($1010 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$), and r_a is aerodynamic resistance. Values of r_a were also calculated using the method from Campbell and Williamson (1997), which firstly required calculation of the aerodynamic resistance to momentum transfer from the measurement height to the canopy (r_{aM}):

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$$r_{aM} = \frac{u}{u_*^2} \quad (5)$$

where u is the horizontal wind speed and u_* is the friction velocity measured by the sonic anemometer.

Then, r_a was calculated as:

$$r_a = \frac{1.6}{k u_*} + r_{aM} \quad (6)$$

210 where k is von Karman's constant (0.4).

2.2.4 Energy balance closure

Energy balance closure was imperfect at both sites, with 84% closure at Kopuatai and 89% at Mer Bleue (Appendix C). This could be due to a number of factors, such as mismatch between EC footprint characteristics for the turbulent and non-turbulent energy balance terms, or increasing uncertainty of surface soil heat flux measurements due to peat accumulation, which
215 increases the depth of soil heat flux plates over time. Energy imbalances could also be a result of a lack of sustained turbulence at these sites (Anderson and Wang, 2014), or due to the use of MoD means of energy balance components rather than 24-hour means (Leuning et al., 2012).

All analyses were carried out using MATLAB R2021b.

220 3 Results

3.1 Climate and hydrology

Mean annual precipitation (P) was $1213 \pm 147 \text{ mm}$ ($\pm 95\%$ confidence interval) at Kopuatai (2012–2022), compared to $879 \pm 58.1 \text{ mm}$ at Mer Bleue (1999–2018). Mean monthly P ranged between 49–139 mm and 50–100 mm at Kopuatai and

Mer Bleu, respectively, with the minimum monthly P occurring during the warm season at Kopuatai and the cool season at Mer Bleu (Fig. 2a). The mean monthly air temperature (T_{air}) range was much smaller at Kopuatai (9.3–19.0 °C) than at Mer Bleu (–10.0–20.2 °C) (Fig. 2b), with mean annual temperatures of 14.1 ± 0.27 °C and 6.2 ± 0.31 °C at the two sites, respectively. Mean annual VPD was 0.39 ± 0.013 kPa at Kopuatai and 0.38 ± 0.023 kPa at Mer Bleu, and monthly mean VPD ranged between 0.17–0.68 kPa and 0.07–0.77 kPa (Fig. 2c). Mean annual WTD was -82.6 ± 14.4 mm at Kopuatai and -377 ± 19.8 mm at Mer Bleu. Monthly mean WTD had a narrower range and was shallower at Kopuatai than at Mer Bleu year-round; as a result, the WTD ranges at these sites did not overlap (–153 to –28 mm and –460 to –278 mm, respectively; Fig. 2d).

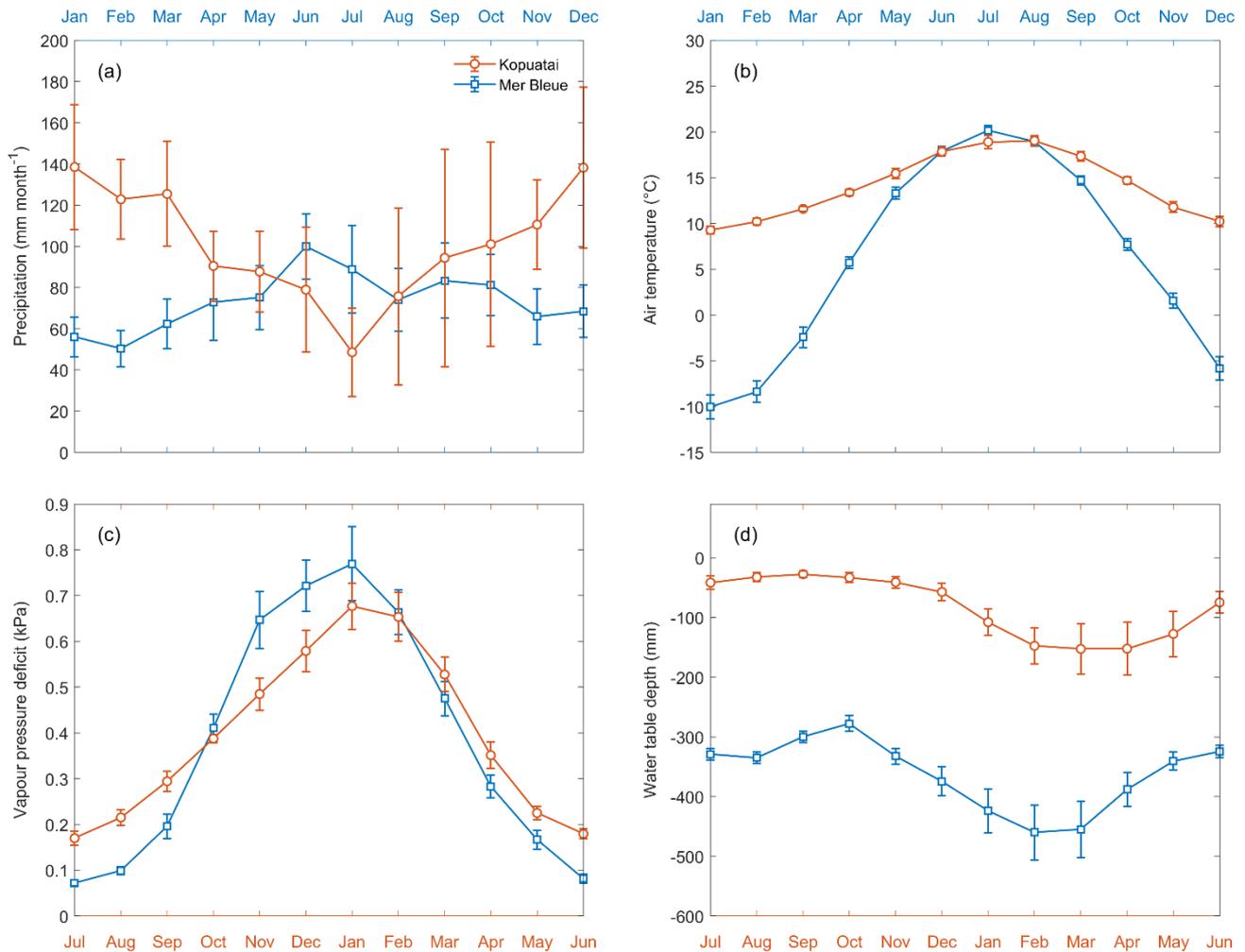


Figure 2. Mean monthly (a) precipitation (b) air temperature (c) vapour pressure deficit, and (d) water table depth at Kopuatai (orange) and Mer Bleu (blue). These values were calculated using data between 2012–2022 (inclusive) at Kopuatai and 1999–2018

235 (inclusive) at Mer Bleue. Error bars are 95% confidence intervals. Note that the Northern and Southern Hemisphere seasons have been aligned by using separate x -axes for each site (Jan–Dec for Mer Bleue and Jul–Jun for Kopuatai).

3.2 Evaporation and equilibrium evaporation

Mean annual E and E_{eq} were larger at Kopuatai compared to Mer Bleue, however, mean annual E/E_{eq} was lower at Kopuatai (Table 1). In addition, growing season and year-round mean E/E_{eq} values were very similar at each respective site. At both sites, mean monthly E was less than E_{eq} , except during winter (Fig. 3). Both variables followed an expected seasonal pattern of low values in winter and high values in summer, mostly driven by the amount of radiation received. The difference between E_{eq} and E was larger at Kopuatai than at Mer Bleue in non-winter months; the maximum difference between monthly E_{eq} and E was 71 mm in January at Kopuatai, but only 21 mm in May at Mer Bleue. Both E and E_{eq} were close to zero at Mer Bleue during winter (Dec–Feb), when T_{air} was below 0 °C and the bog was snow-covered, and both values were similar during spring (March) and autumn (October) months.

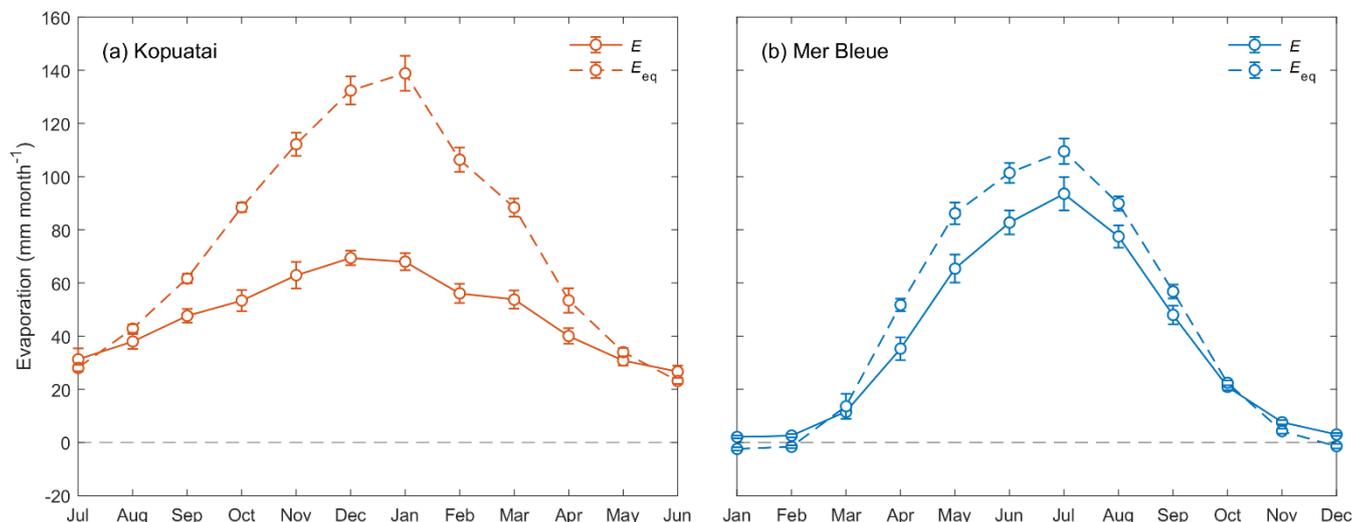
Table 1. Mean annual ecosystem evaporation (E) and equilibrium evaporation (E_{eq}), with means and ranges of their ratios (i.e. Priestley–Taylor α) at each site ($n = 11$ and 20 years for Kopuatai and Mer Bleue, respectively). These values are given for both year-round data and for the growing season only (Sep–May at Kopuatai and May–Oct at Mer Bleue). Values in parentheses are 95% confidence intervals.

Site	Annual				Growing season only			
	E (mm)	E_{eq} (mm)	E/E_{eq}	E/E_{eq} range	E (mm)	E_{eq} (mm)	E/E_{eq}	E/E_{eq} range
Kopuatai	578 (± 13)	910 (± 18)	0.64 (± 0.022)	0.57–0.70	482 (± 11)	816 (± 19)	0.59 (± 0.023)	0.52–0.65
Mer Bleue	450 (± 17)	530 (± 13)	0.85 (± 0.026)	0.76–0.95	388 (± 16)	466 (± 11)	0.83 (± 0.027)	0.70–0.94

3.3 Dry canopy energy balance partitioning

Seasonal energy balance partitioning was markedly different at each site. At Kopuatai, H was greater than LE in most months, with LE only comprising 21% of annual R_n (Fig. 4). During autumn and winter (April to August), however, the difference between H and LE was smaller. In contrast, LE was a much larger component of the energy balance at Mer Bleue, representing

43% of the annual R_n due to LE exceeding H throughout most of the growing season. During the rest of the year, however, LE was either less than or similar to H . There was also a difference in the seasonality of LE , H , and R_n between sites – at Kopuatai, all components of the energy balance reached a maximum during summer; LE and R_n peaked in mid-summer (January), while H peaked a month earlier. At Mer Bleue, LE and R_n also peaked during summer (in June and July, respectively), however H peaked in the middle of spring (April).

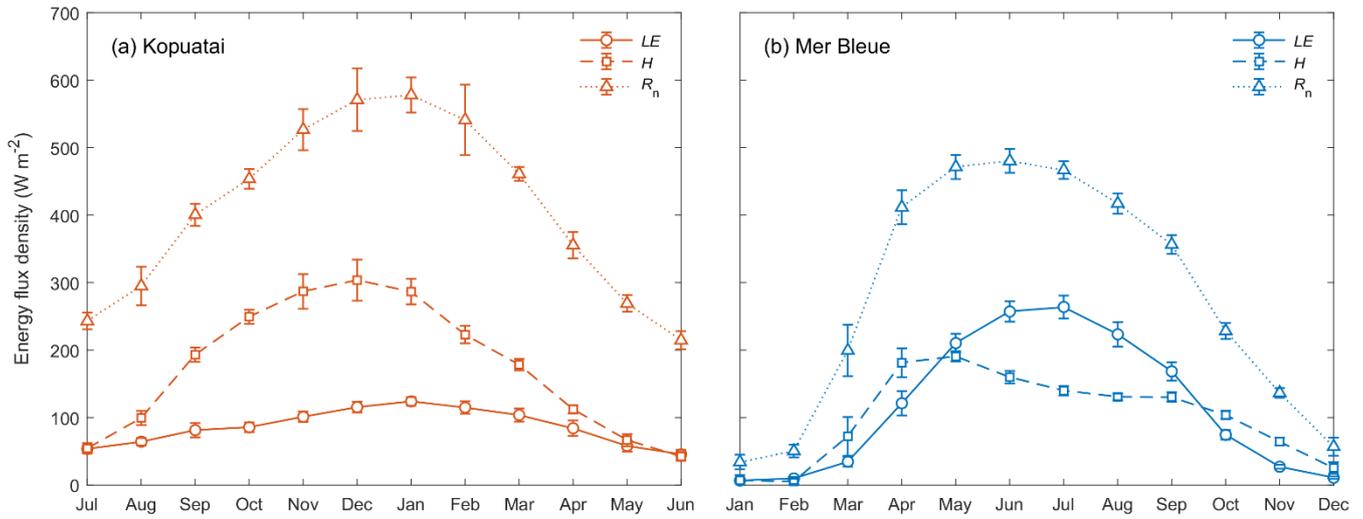


265 **Figure 3. Mean monthly evaporation (E) and equilibrium evaporation (E_{eq}) at (a) Kopuatai and (b) Mer Bleue. Error bars represent 95% confidence intervals. Note that the x -axis for Kopuatai in the Southern Hemisphere starts from July (a six-month offset from the graph for Mer Bleue in the Northern Hemisphere).**

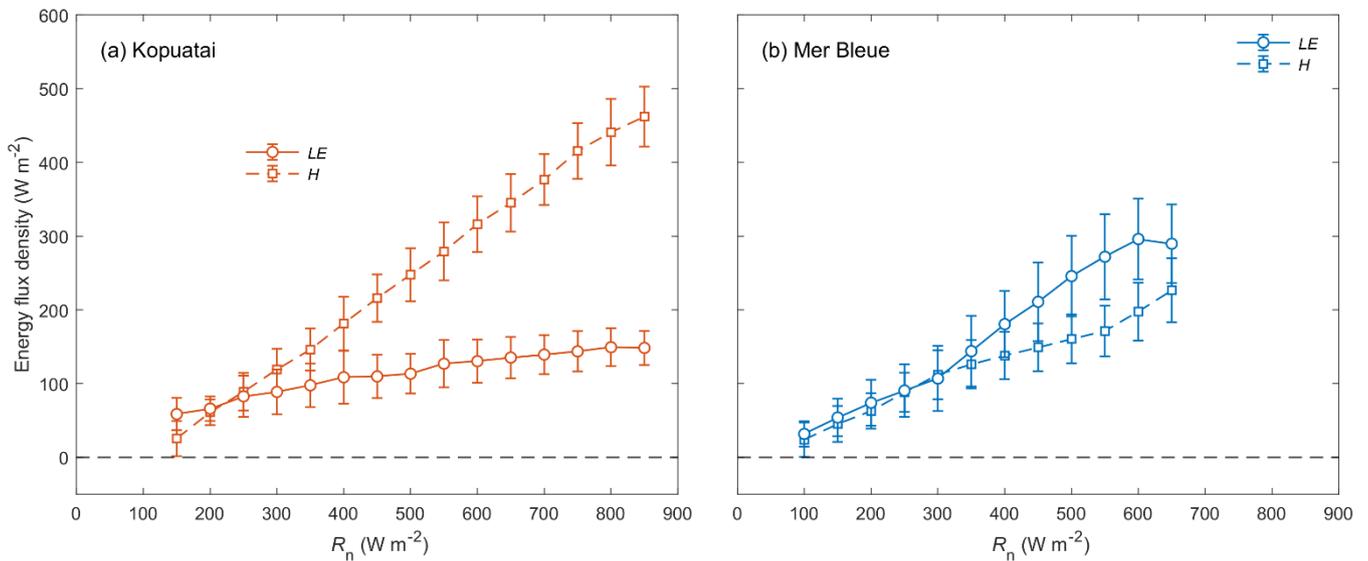
Mean monthly LE increased substantially (monthly range = 257 W m^{-2}) towards summer at Mer Bleue, while at Kopuatai, there was less monthly variation in LE (range = 79 W m^{-2}). Although maximum monthly R_n ($\pm 95\%$ confidence interval) at Kopuatai was higher than at Mer Bleue ($578 \pm 26.0 \text{ W m}^{-2}$ and $480 \pm 17.7 \text{ W m}^{-2}$, respectively), maximum monthly LE at Kopuatai ($124 \pm 6.45 \text{ W m}^{-2}$) was lower relative to Mer Bleue ($264 \pm 17.0 \text{ W m}^{-2}$). Consequently, maximum monthly H was higher at Kopuatai than at Mer Bleue ($304 \pm 30.5 \text{ W m}^{-2}$ and $191 \pm 7.57 \text{ W m}^{-2}$, respectively). In addition, R_n was particularly low in winter at Mer Bleue due to snow cover increasing albedo, and the lower solar receipt. During spring, R_n increased steeply (March and April) due to a decrease in albedo following snowmelt. In contrast, Kopuatai does not receive snow, and seasonal albedo of the evergreen plant canopy hardly varies (not shown).

Middle-of-day mean energy balance partitioning during dry canopy conditions was also distinctly different between Kopuatai and Mer Bleue (Fig. 5). At Kopuatai, H was a much larger component of the energy balance than LE (Fig. 5a); H was greater than LE at $R_n \geq 450 \text{ W m}^{-2}$, which was reflected in a mean Bowen ratio (β) of 2.0 (β range based on binned H and LE values

280 was 0.43–3.11). At Mer Bleue, however, LE was either similar to or greater than H (Fig. 5b). As a result, mean β was 0.80, with a range of 0.63–1.05.



285 **Figure 4. Mean monthly energy balance partitioning (latent heat flux, LE , sensible heat flux, H , and net radiation, R_n) at (a) Kopuatai and (b) Mer Bleue for middle-of-day, dry canopy conditions. Error bars are 95% confidence intervals. Note that the x-axis for Kopuatai in the Southern Hemisphere starts from July (a six-month offset from the graph for Mer Bleue in the Northern Hemisphere).**



290 **Figure 5. Relationship between binned mean middle-of-day latent and sensible heat fluxes (LE and H) versus net radiation (R_n) for dry canopy conditions at (a) Kopuatai and (b) Mer Bleue. Values are for the growing season only (Sep–May at Kopuatai and May–Oct at Mer Bleue). Error bars are standard deviations.**

3.4 Wet canopy energy balance partitioning

During wet canopy conditions, the limitation on LE observed at Kopuatai under dry canopy conditions was not apparent (Fig. 6a); LE was greater than H at both low and high R_n in these conditions (β ranged between 0.01–0.94, with a mean of 0.48). Both LE and H increased at approximately the same rate with increasing R_n . At Mer Bleue, the relationship between LE , H , and R_n under wet canopy conditions appeared similar to dry canopy conditions, with a lower mean β of 0.58 and a range of –0.37–0.85 (Fig. 6b).

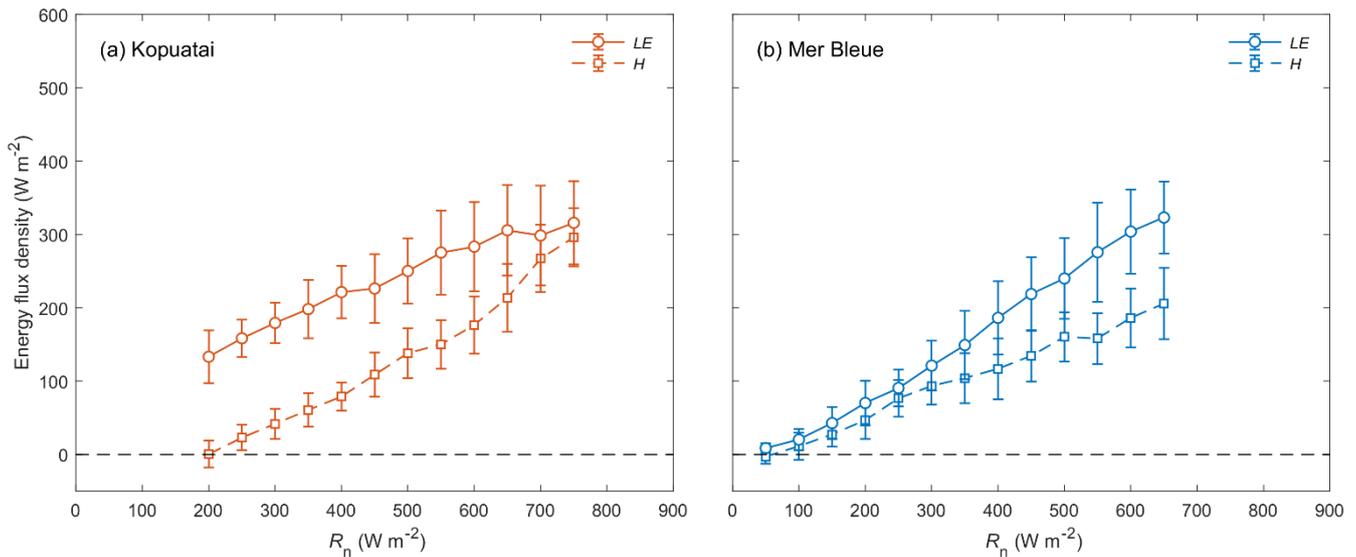


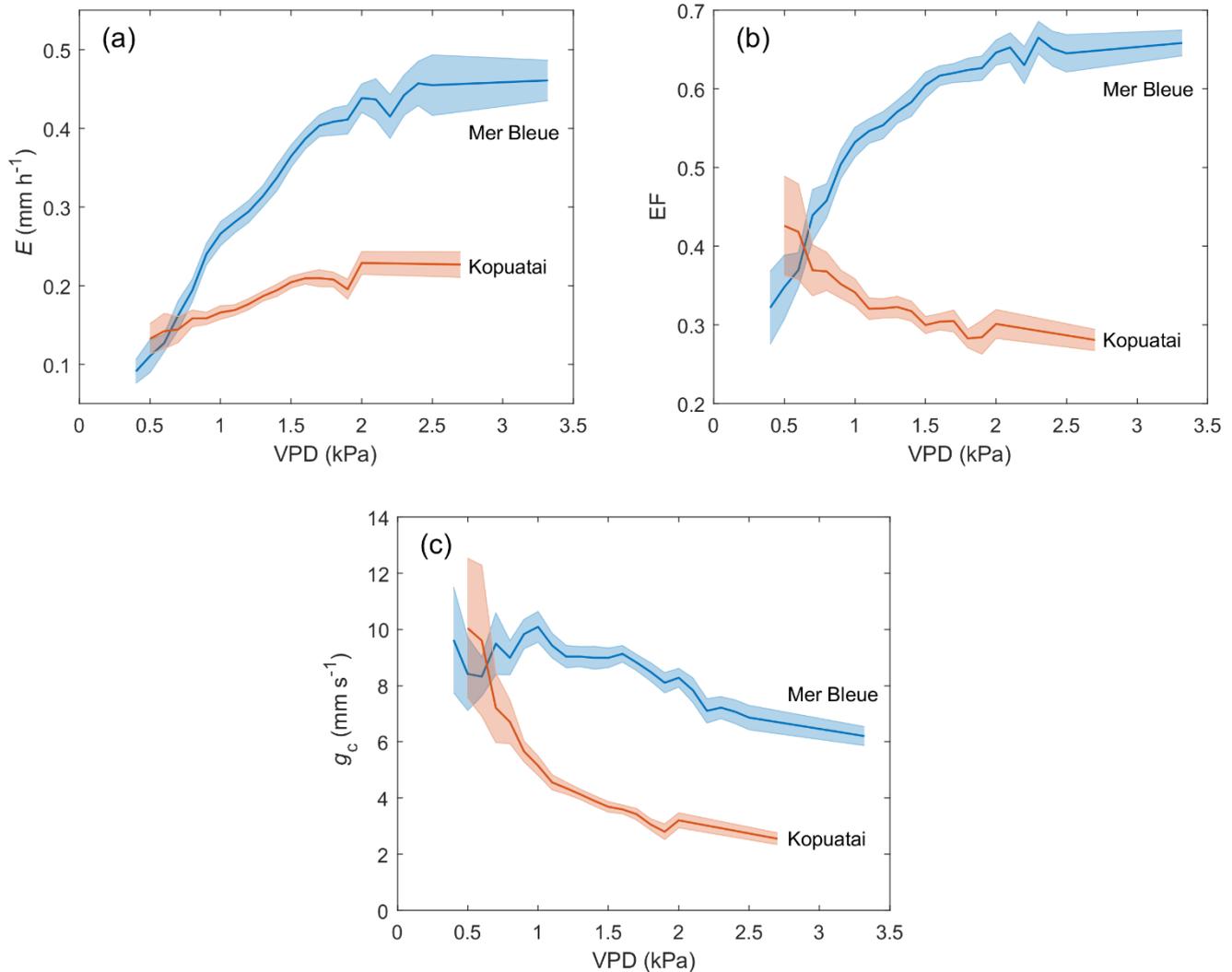
Figure 6. Relationship between binned mean middle-of-day latent and sensible heat fluxes (LE and H) versus net radiation (R_n) for wet canopy conditions at (a) Kopuatai and (b) Mer Bleue. Values are for the growing season only (Sep–May at Kopuatai and May–Oct at Mer Bleue). Error bars are standard deviations.

3.5 Response of E , EF , and g_c to VPD

Dry canopy E rates increased with increasing VPD at both sites, i.e. greater water loss occurred at high VPD (Fig. 7a). For $VPD < 2.0$ kPa, the rate of increase in E with increasing VPD was 3.4 times larger at Mer Bleue ($0.217 \text{ mm h}^{-1} \text{ kPa}^{-1}$) than at Kopuatai ($0.064 \text{ mm h}^{-1} \text{ kPa}^{-1}$). This resulted in a higher E rate of 0.44 mm h^{-1} at $VPD = 2.0$ kPa at Mer Bleue, compared to only 0.23 mm h^{-1} at the same VPD at Kopuatai. Beyond $VPD = 2.0$ kPa, E showed little or no change with increasing VPD at both sites.

At Kopuatai, EF decreased in response to increasing VPD, while the opposite trend was observed at Mer Bleue (Fig. 7b). These contrasting responses of EF to increasing VPD were also evident in 30-minute data (Appendix D). At Kopuatai, mean daytime EF decreased from 0.43 at $VPD = 0.5$ kPa to 0.28 at 2.7 kPa, and increased from 0.32 at 0.4 kPa to 0.66 at 3.3 kPa at Mer Bleue. At both sites, the rate of increase or decrease in EF was reduced at $VPD > 1.0$ kPa.

There was a steep decline in g_c with increasing VPD at Kopuatai (Fig. 7c); mean g_c decreased from a maximum of 10.0 mm s^{-1} at a VPD of 0.5 kPa to a minimum of 2.55 mm s^{-1} at 2.7 kPa . In contrast, the pattern of declining g_c with increasing VPD was weak at Mer Bleue, decreasing from 9.63 mm s^{-1} at 0.4 kPa to 6.20 mm s^{-1} at 3.3 kPa .



320

Figure 7. Middle-of-day mean growing season (a) evaporation (E), (b) evaporative fraction (EF), and (c) canopy conductance (g_c) for 0.1 kPa bins of vapour pressure deficit (VPD) during dry canopy conditions at Kopuatai and Mer Bleue. Shaded areas represent 95% confidence intervals.

325

4 Discussion

330 4.1 Evaporation regimes

Our study demonstrates the crucial importance of vegetation characteristics in controlling water losses from peatlands. Kopuatai and Mer Bleue, two ombrotrophic bogs with different vegetation communities, display strikingly different evaporation regimes, energy balance partitioning, and responses of E , EF , and g_c to VPD. Despite being in a warmer climate zone with warm winters, the E regime at Kopuatai was more conservative than at Mer Bleue. Although mean annual E and E_{eq} were 25% and 53% higher at Kopuatai than at Mer Bleue, mean annual E/E_{eq} was 28% lower at Kopuatai. This occurred because mean annual E was 45% lower than mean annual E_{eq} at Kopuatai, while at Mer Bleue there was only a 16% difference. The large difference between E and E_{eq} at Kopuatai occurred due to conservative E , as well as the relatively high E_{eq} resulting from higher R_n (due to latitudinal differences), a warmer climate, and longer growing season compared to Mer Bleue. These results indicate that greater surface limitations were imposed on E at Kopuatai relative to Mer Bleue. The difference in E/E_{eq} between the two sites is highly likely to be a result of differences in functional vegetation types, as different vegetation communities, even at the same peatland, have been shown to result in contrasting E regimes (Takagi et al., 1999; Strilesky and Humphreys, 2012). As such, the substantial limitations on E observed at Kopuatai likely occurred due to the physiological and canopy structural features of the dominant vascular plant, *E. robustum*. However, some limitation on E was observed at Mer Bleue, as evidenced by the decrease in E/E_{eq} towards mid-summer. It is possible that this occurred due to stomatal closure in the shrub vegetation in response to high VPD (Admiral et al., 2006). However, the impact of this limitation was weaker than at Kopuatai, likely due to high surface E from *Sphagnum* carpets at Mer Bleue (Admiral et al., 2006).

At Kopuatai, the entire range of E/E_{eq} values tended to be lower than at most Northern Hemisphere peatlands, while the E/E_{eq} range at Mer Bleue overlapped with the lower end of most of these ranges (Table 2; we could not find equivalent studies for Southern Hemisphere peatlands). However, there were some northern peatland sites with E/E_{eq} ranges that were closer to those of Kopuatai. For example, a tree-dominated peatland in Canada had a lower E/E_{eq} than at Kopuatai, which could be attributed to stomatal limitation of transpiration (Brümmer et al., 2012), i.e., the same mechanism of E limitation as exhibited at Kopuatai, but to a greater extent. Of interest is also the Fäjemyr bog in Sweden, which had lower growing season E/E_{eq} values than most peatlands in Table 2 (but not Kopuatai), possibly due to a low water table and low surface conductance (Alekseychik et al., 2018). In addition, in an earlier study of E rates at Kopuatai, Thompson et al. (1999) reported lower E/E_{eq} values than those in this study; this likely occurred because measurements were made only during summer, when limitations on E are most prominent. Apart from these outliers, the E/E_{eq} values for Northern Hemisphere peatlands in Table 2 are generally much greater than at Kopuatai bog, indicating that *E. robustum* may be more adept at restricting E than the vascular and non-vascular vegetation in most northern peatlands.

360 **Table 2. Summary of studies reporting the ratio of evaporation to equilibrium evaporation (E/E_{eq}) for peatlands globally (including this study), with a description of the type of variability covered in the range of E/E_{eq} values, and the time period for which they were calculated.**

Location	Dominant vegetation types	E/E_{eq}	Range type	Time period	Reference
Kopuatai bog, Aotearoa New Zealand	<i>Empodisma robustum</i>	0.57–0.70	Interannual variability	Year-round	This study
		0.52–0.65	Interannual variability	Growing season (Sep–May)	This study
	<i>Empodisma robustum</i>	0.34	N/A	Growing season (Nov–Mar)	Thompson et al. (1999)
	<i>Sporadanthus ferrugineus</i> ^a	0.58	N/A	Summer period (Jan–Mar)	Thompson et al. (1999)
Mer Bleue bog, Canada	Shrubs and <i>Sphagnum</i> moss	0.76–0.95	Interannual variability	Year-round	This study
		0.70–0.94	Interannual variability	Growing season (May–Oct)	This study
Plotnikovo, Russia	Sedges, shrubs, and <i>Sphagnum</i> moss	0.99–1.29 (1999) 0.96–1.07 (2000)	Seasonal variability	Growing season (Apr–Oct)	Shimoyama et al. (2004)
Sandhill fen, Canada	Trees, shrubs, and brown moss	0.79–1.04	Interannual variability	Snow-free periods (May–Nov)	Sonnentag et al. (2010)
Alberta, Canada	Trees, shrubs, and various mosses	0.55–0.57	Interannual variability	Year-round	Brümmer et al. (2012)
Degerö Stormyr, Sweden	Shrubs, grasses, and <i>Sphagnum</i> moss	0.86–1.17	Interannual variability	Year-round	Peichl et al. (2013)
Siikaneva-1 & Siikaneva-2, Finland	Shrubs, sedges, and <i>Sphagnum</i> moss	1.09–1.21 & 1.11–1.13	Interannual variability	Growing season (May–Oct)	Alekseychik et al. (2018)
Fäjemyr bog, Sweden	Shrubs, sedges, <i>Sphagnum</i> moss, and sparse trees	0.66–0.71	Interannual variability	Growing season (May–Oct)	Alekseychik et al. (2018)
Seven peatlands in Canada	Shrubs, sedges, mosses (all peatlands), trees, and herbs (some peatlands)	0.82–1.05	Spatial variability	Midsummer period (Jul–Aug)	Humphreys et al. (2006)

^a A late-successional tall restiad plant that dominates portions of Kopuatai bog, but is not present at the EC site.

4.2 Controls on evaporation

Our analysis focused on VPD as the driver of changes in E , EF , and g_c . However, VPD is strongly driven by T_{air} and humidity, with T_{air} , in turn, responding strongly to solar radiation via the surface radiation balance (Chang & Root, 1975; Grossiord et al., 2020). Disentangling the drivers of water vapour fluxes in vegetated environments is therefore challenging. At Kopuatai bog, Goodrich et al. (2015) used modified light-response models to disentangle the primary seasonal drivers of gross primary production (GPP) for the *E. robustum* canopy. Summertime GPP was strongly limited under high VPD conditions rather than high T_{air} , which they concluded was due to VPD-induced stomatal closure, implying that the transpiration component of E would be affected by changes in VPD. This variable has also been observed to drive stomatal response in other wetland settings (Takagi et al., 1998; Aurela et al., 2007; Otieno et al., 2012).

The steep decline in EF with increasing VPD at Kopuatai suggests strong surface controls on E . A similar negative relationship between midsummer LE/R_n and VPD was shown by Takagi et al. (1999) at a section of a peatland invaded by vascular vegetation, which was attributed to stomatal closure. This is also likely to be the main factor limiting E from Kopuatai due to the non-linear decrease in canopy conductance (g_c) with increasing VPD, a trend that has also been observed in other peatlands (Humphreys et al., 2006; Peichl et al., 2013; Runkle et al., 2014; Alekseychik et al., 2018). However, it has also been hypothesised that the standing litter layer formed by *E. robustum* reduces E (Campbell and Williamson, 1997); this canopy feature has been observed to limit E in marsh, restored wetland, and dryland ecosystems (Goulden et al., 2007; Villegas et al., 2010; Eichelmann et al., 2018). Standing litter restricts E by decoupling the subcanopy environment from atmospheric turbulence and by preventing solar radiation from reaching the surface, which minimises the variability of T_{air} and VPD below the litter layer (Goulden et al., 2007; Eichelmann et al., 2018). Although we cannot separate the effects of stomatal closure and standing litter on E , it is likely that both of these factors act in tandem to severely restrict E at Kopuatai.

At Mer Bleue, E rates were almost double those of Kopuatai at high VPD, and there was a greater absolute increase in dry canopy LE with increasing R_n at Mer Bleue than at Kopuatai (an increase of 254 W m^{-2} compared to 93 W m^{-2} , respectively), indicating weaker water loss restrictions at Mer Bleue. Weak restrictions likely occurred because of the large contribution of *Sphagnum* moss E during well-watered conditions, as moss E is enhanced substantially by increasing VPD (Admiral and Lafleur, 2007). Since LE increased with increasing R_n , and E and EF increased with increasing VPD, both of these factors were important controls on E and energy partitioning at Mer Bleue. Similar positive correlations between LE and R_n (or available energy, $R_n - G$) at daily and monthly scales have previously been observed at other peatlands (Lafleur and Roulet, 1992; Kurbatova et al., 2002; Brümmer et al., 2012), in addition to positive relationships between daily E and VPD (Wu et al., 2010; Peichl et al., 2013; Wang et al., 2020).

There were also reduced rates of increase in E and EF with increasing VPD at Mer Bleue (i.e., a ‘saturating’ effect; also observed in data presented by Peichl et al., 2013), which only became evident at high VPD (above ~2.0 kPa for E and
400 ~1.0 kPa for EF ; Fig. 7). This relatively weak E limitation was likely caused by stomatal control of transpiration by vascular
vegetation (Admiral et al., 2006), as a slight decrease in g_c was observed with increasing VPD. A similar relationship between
surface conductance and VPD has previously been observed at Mer Bleue (Humphreys et al., 2006). It has also been suggested
that E may become limited at high VPD if the transport rate of water through mosses is insufficient to meet the atmospheric
demand (Liljedahl et al., 2011). While we cannot determine whether this occurred at Mer Bleue using the data available, it is
405 possible that this may have been a contributing factor to limitations on E .

While there was almost no difference in energy balance partitioning between dry and wet canopy conditions at Mer Bleue, the
canopy wetness state had a major effect at Kopuatai. During dry canopy conditions, H was the dominant convective flux, as
the rate of increase in LE with increasing R_n was suppressed. However, LE became dominant over H during wet canopy
410 conditions, with a much greater rate of increase in LE with increasing R_n compared to dry canopy conditions. A previous study
at Kopuatai also reported dominance of LE over H when the canopy was rain-wetted, and vice versa during dry canopy
conditions (Campbell and Williamson, 1997). This contrast in energy partitioning likely occurred due to suppression of E from
the moist peat surface by the dense standing litter layer of *E. robustum* during dry canopy conditions.

415 The responses of E and EF to increasing VPD at Mer Bleue were consistent with previous findings by Helbig et al. (2020),
which synthesised data from 35 boreal peatlands, including Mer Bleue; however, the response at Kopuatai bog was closer to
that of the boreal forests included in their study. As such, the response of E to VPD at Kopuatai bog is distinctive compared to
boreal peatlands. This may be a critical adaptation that allows peat formation in a climate zone that is uncharacteristic for
ombrotrophic peatlands (McGlone, 2009) due to the combination of moderate precipitation and a higher mean annual
420 temperature than at Northern Hemisphere peatlands. Tropical peatlands also experience higher temperatures, however annual
precipitation tends to be much higher than at Kopuatai (>2500 mm in Southeast Asia, for example; Page et al., 2006), which
enables wet conditions to be maintained. Therefore, it is likely that the dominance of *E. robustum* at Kopuatai is crucial to the
persistence of this peatland in an atypical peatland climate zone due to restrictions imposed on transpiration and sub-canopy
 E , as these adaptations likely contribute to maintaining a shallow and stable water table.

425 **4.3 Implications for future peatland water balances**

Northern Hemisphere peatlands, such as Mer Bleue, may be at risk of increased evaporative water loss as VPD increases due
to climate warming (Helbig et al., 2020). This could lead to more frequent low water tables and water deficits, which in turn
may reduce net C uptake (Zhong et al., 2020; Kwon et al., 2022). The effect of low water tables on the C balance has previously
been observed at Mer Bleue, where lowering of water levels at a beaver pond near the EC site caused a decrease in C uptake;

430 further modelling also predicted that a beaver pond water table below ~1.7 m would cause Mer Bleue to switch from a C sink to a source (He et al., 2022). Similar impacts were observed at Kopuatai during a severe drought in 2013, where monthly total ecosystem respiration increased in response to a slightly deeper water table, leading to a small reduction in the annual net C balance (Goodrich et al., 2017). At a drainage-affected bog near Kopuatai, multi-year data indicated that the water table was substantially lower year-round and caused lower C uptake rates compared to Kopuatai, but likely remained a C sink due to the
435 tolerance of *E. robustum* to a low and fluctuating water table (Ratcliffe et al., 2019). Therefore, C uptake at both Kopuatai and Mer Bleue could be impacted by decreased water tables; however, under increased VPD due to climate warming, it appears that Kopuatai may be able to retain more water than Northern Hemisphere peatlands through strong constraints on *E*. This greater water retention at Kopuatai could enable current high and stable net annual C uptake rates (Goodrich et al., 2017) to be maintained despite warmer and potentially drier conditions in the future (Lawrence et al., 2022). Therefore, we propose that
440 the previously observed resilience of C uptake at Kopuatai to dry conditions (Goodrich et al., 2017) primarily results from “hydrological resistance” to increasing VPD driven by the water conservative properties of the *E. robustum* canopy.

5 Conclusions

We compared ecosystem *E* regimes, energy balance partitioning, and the response of *E* to VPD at two peatlands – Kopuatai bog in Aotearoa New Zealand and Mer Bleue bog in Canada. Our motivation was to determine whether regulation of water
445 losses in these peatlands with different vegetation communities enables hydrological resistance to climatic drying. Our results demonstrated that the *E* regime was much more conservative at Kopuatai than at Mer Bleue at high VPD, likely due to restrictions imposed on g_c by the dominant vegetation species, *E. robustum*. At Mer Bleue, *E* was only weakly limited at high VPD, as the impacts of reduced shrub g_c were likely offset by water loss from non-vascular moss surfaces. The greater limitations on *E* observed at Kopuatai indicate hydrological resistance of this vascular plant-dominated ecosystem to hydro-
450 climatic change. Importantly, this resistance likely contributes to resilience of the net C sink at Kopuatai, despite being located in a warm-temperate climate zone, and is thus a key self-regulation mechanism. As a result, it appears that Kopuatai may be better equipped to conserve water and maintain high net C uptake rates than Mer Bleue, and perhaps other Northern Hemisphere peatlands, in the face of climate change-induced warming and drying. Further investigation of *E* partitioning into transpiration, interception loss, and peat surface *E*, and the role of the dense standing litter layer for *E* regulation at Kopuatai
455 may yield additional insights into this observed hydrological resistance.

Appendices

Appendix A

Table A1. Methods and instruments used for data collection at Kopuatai and Mer Bleue.

Variable	Kopuatai	Mer Bleue
Latent heat flux (LE)	4.25 m CSAT3 & CSAT3B (CSI); LI-7500 (LI-COR)	3.0 m 1012R3 & R3-50 (Gill); LI-6262 & LI7000 (LI-COR)
Sensible heat flux (H)	4.25 m CSAT3 & CSAT3B (CSI)	1012R3 & R3-50 (Gill)
Soil (peat) heat flux (G)	HFP01 (Hukseflux); TCAV (CSI)	N/A
Net radiation flux density (R_n)	2 m NR01 (Hukseflux)	CNR1 (Kipp & Zonen)
Air temperature (T_{air}) and vapour pressure deficit (VPD)	4.2 m HMP155 (Vaisala)	2 m HMP various models (Vaisala)
Precipitation (P)	0.6 m TB03 (Hydrological Services)	0.3 m TM525 tipping bucket gauge (Texas Instruments) Winter snowfall from Environment Canada weather station at Ottawa Airport
Water table depth (WTD)	Dipwell, WL1000 (Hydrological Services)	Float & potentiometer, and OTT PLS

Appendix B

The antecedent precipitation index (API) is an exponential function used to predict the duration of canopy wetness after a rainfall event, with inputs of rainfall depth and time since rainfall (Keyte Beattie, 2014). Initially conceived by Woods and Rowe (1996) for predicting catchment moisture conditions prior to a rain event, the API function was then modified by Smith (2003) to estimate canopy wetness state:

$$\text{API} = \sum_{i=1}^j \frac{P_i}{1.104 \times 1.024^i} \quad (\text{B1})$$

where P_i is precipitation (mm) measured during the i^{th} half-hour period before the current half hour, and j is the moving window size in half hours (48 in this study). An example of modelled canopy drying using the API function is shown in Fig. B1. An API value of 0.2 units or less approximately represents a dry canopy, meaning that E is predominantly sourced from peat surface E and transpiration. When the API value is greater than or equal to 1, the vegetation canopy is wet and interception loss is the dominant source of E .

Predictions of canopy wetness using API have been shown to correspond reasonably well with leaf wetness sensor measurements at Kopuatai, using an API period of 18 hours for the upper canopy, 36 hours for the standing litter layer, and 60 hours for the lower canopy (Keyte Beattie, 2014). In this study, we defined wet canopy periods as times when the upper canopy was saturated, i.e., when interception loss likely made up the majority of E , so an 18-hour API period would likely be appropriate for this study. However, in order to conservatively identify periods with a dry upper canopy, i.e., for greater certainty that the canopy is dry when $\text{API} \leq 0.2$, a slightly longer period of 24 hours was used. While this approach has only been tested in the field at Kopuatai, for consistency we used the same function for separating wet and dry canopy measurements at Mer Bleue. Given the relatively sparse shrub canopy and absence of standing litter at Mer Bleue, API should provide conservative estimates of canopy dryness. The use of MoD data in this study is beneficial as it would have reduced the impact of early morning wetting from dew, therefore reducing the number of instances where API predicted canopy wetness incorrectly.

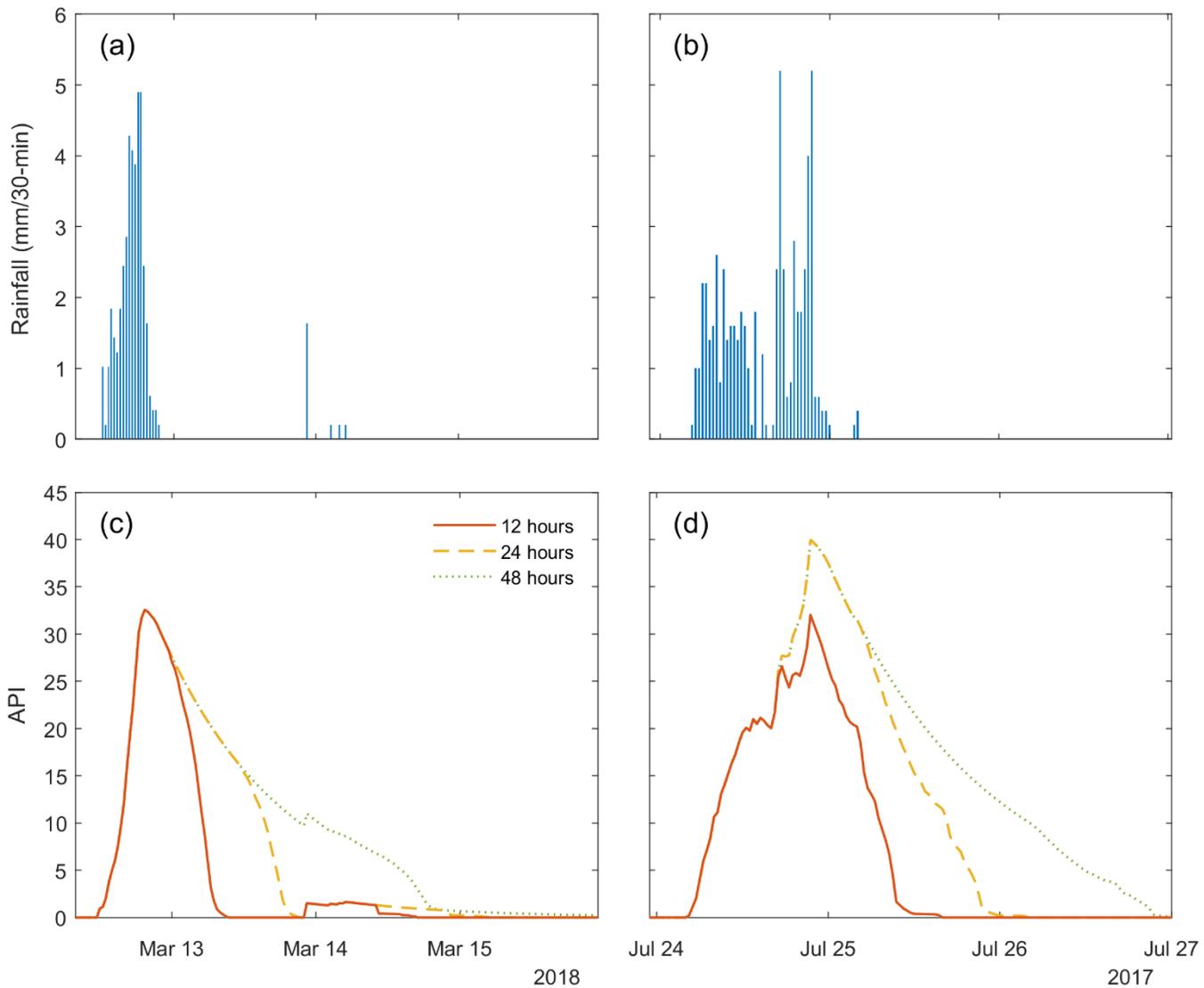
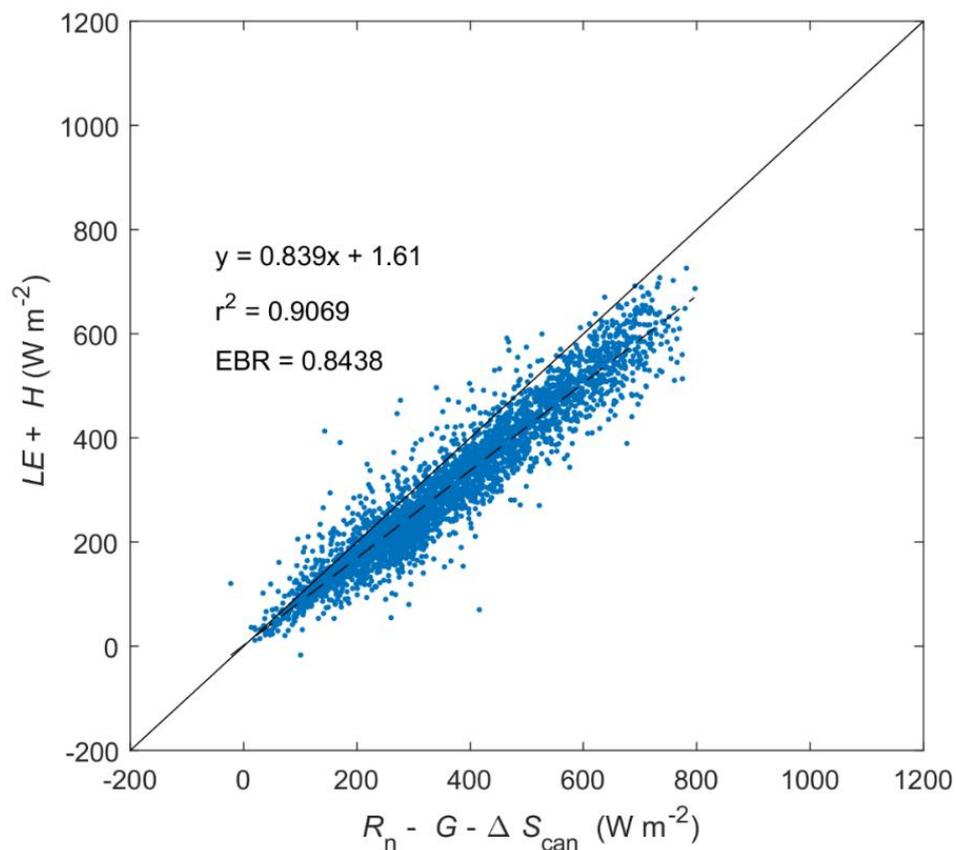


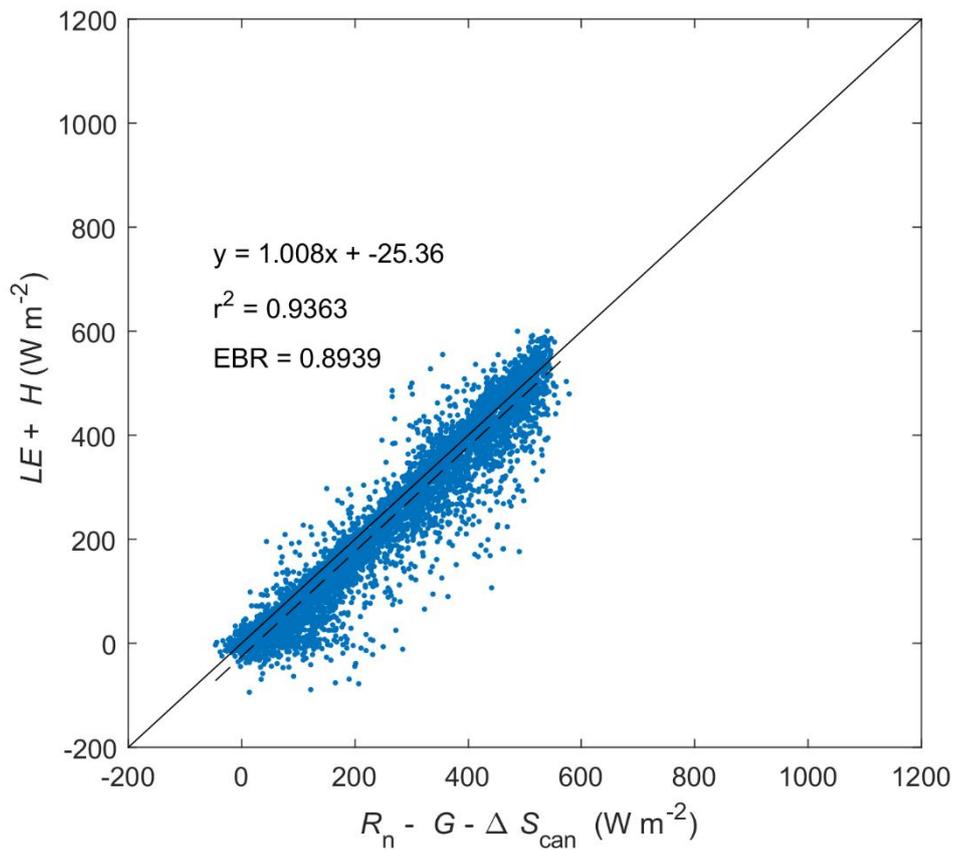
Figure B1. Examples of predicted canopy drying after rainfall using the antecedent precipitation index (API) with 24, 48, and 96 half hour time parameters. The rain event in (a) and (c) is from the Kupuatai dataset, while (b) and (d) consist of Mer Bleue data.

Appendix C



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Figure C1. Energy balance closure at Kopuatai for 2012–2022 (inclusive), based on middle-of-day means of energy balance components. LE : latent heat flux; H : sensible heat flux; G : soil heat flux; R_n : net radiation; ΔS_{can} : canopy heat storage change. EBR is the energy balance ratio.



495 **Figure C2. Energy balance closure at Mer Bleue for 1999–2018 (inclusive), based on middle-of-day means of energy balance components. For term definitions, see Fig. C1. G is assumed to be 10% of R_n , while ΔS_{can} is assumed to be 3% of R_n . EBR is the energy balance ratio.**

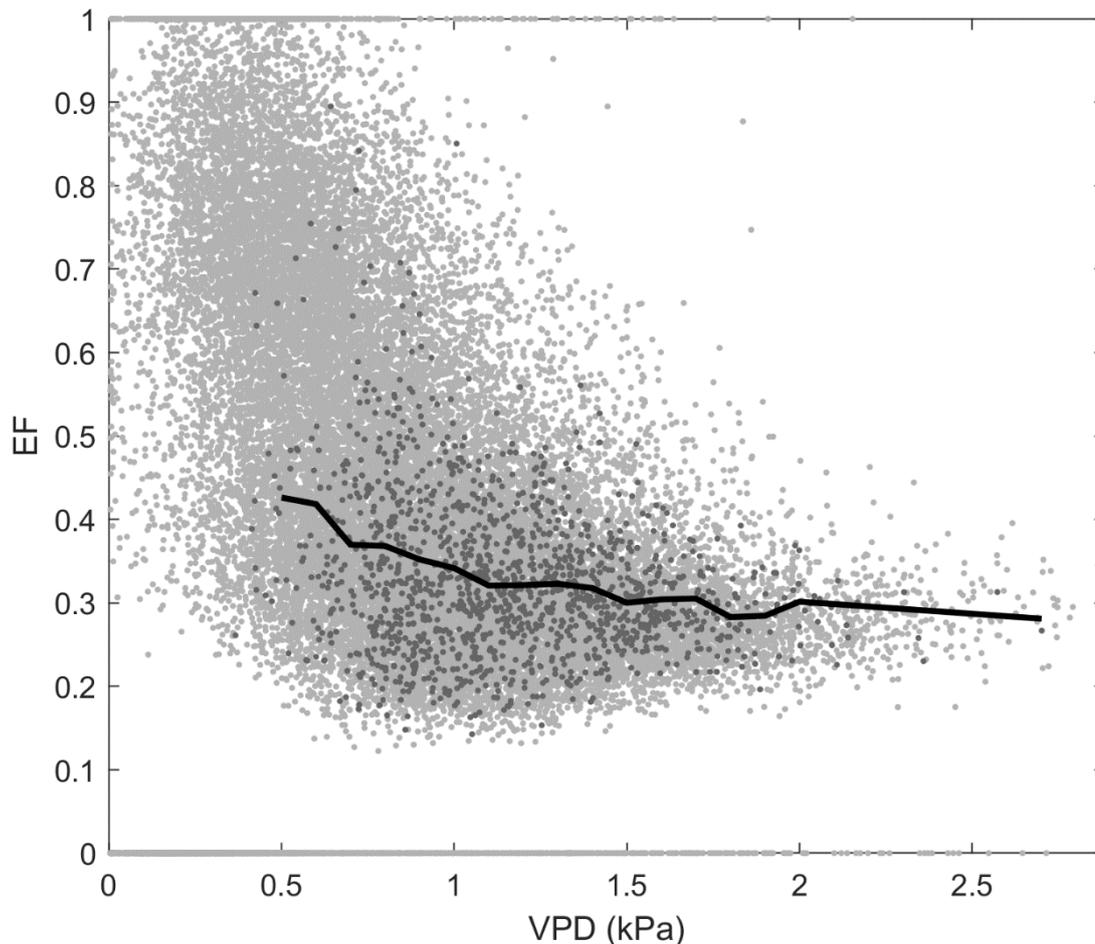
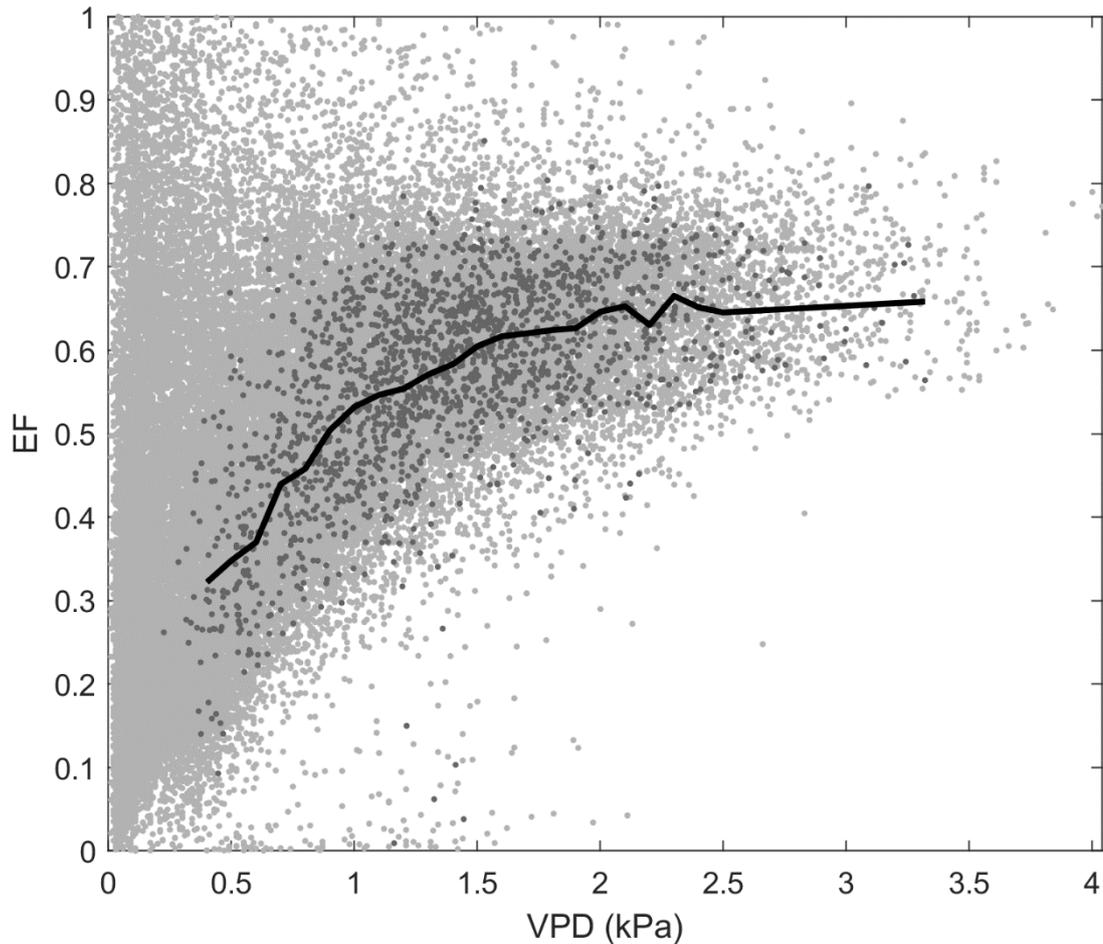


Figure D1. Relationship between evaporative fraction (EF) and vapour pressure deficit (VPD) at Kopuatai bog. Light grey data points represent raw, middle-of-day 30-minute eddy covariance data, while dark grey data points show growing season (Sep–May), dry canopy, middle-of-day mean data used to calculate the binned means (black line).



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Figure D2. Relationship between evaporative fraction (EF) and vapour pressure deficit (VPD) at Mer Bleue bog. Light grey data points represent raw, middle-of-day 30-minute eddy covariance data, while dark grey data points show growing season (May–Oct), dry canopy, middle-of-day mean data used to calculate the binned means (black line).

Data availability

510 Data sets used in this paper are available on Zenodo at <https://doi.org/10.5281/zenodo.8226862> (Speranskaya et al., 2024).

Author contribution

DIC and PML initiated the project and developed the methodology with LS. DIC collected and processed data from Kopuatai, and PML and ERH collected and processed data from Mer Bleue. LS analysed the data and wrote the manuscript draft. DIC, PML, and ERH contributed to review and editing of the manuscript.

515 **Competing interests**

The authors declare that they have no conflict of interest.

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