

1 **Land-surface evapotranspiration derived from a first-principles primary production model**

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13 **Abstract:**

14 We propose an application of eco-evolutionary optimality theory in the context of monitoring and modelling
15 physical land-surface processes. Evapotranspiration (ET) links the water and carbon cycles in the
16 atmosphere, hydrosphere, and biosphere. We develop an ET modelling framework based on the hypothesis
17 that canopy conductance acclimates to plant growth conditions so that the total costs of maintaining
18 carboxylation and transpiration capacities are minimized. This is combined with the principle of
19 co-ordination between the light- and Rubisco-limited rates of photosynthesis to predict gross primary
20 production (GPP). Transpiration (T) is predicted from GPP via canopy conductance. No plant type- or
21 biome-specific parameters are required. ET is estimated from T by calibrating a site-specific (but
22 time-invariant) ratio of modelled average T to observed average ET. Predicted seasonal cycles of GPP were
23 well supported by (weekly) GPP data at 20 widely distributed eddy-covariance flux sites (228 site-years),
24 with correlation coefficients (r) = 0.81 and root-mean-square error (RMSE) = 18.7 gC/week and

25 Nash-Sutcliffe efficiency coefficient (NSE) = 0.61. Seasonal cycles of ET were also well supported, with $r =$
26 0.85, RMSE = 5.5 mm week⁻¹ and NSE = 0.66. Estimated T/ET ratios (0.52–0.92) showed significant
27 positive relationships to radiation, precipitation and green vegetation cover and negative relationships to
28 temperature and modelled T ($r = 0.84$). Although there are still uncertainties to be improved in the current
29 framework, particularly in estimating T/ET, we see the application of eco-evolutionary principles as a
30 promising direction for water resources research.

31 **Keywords:** canopy conductance, evapotranspiration, transpiration, gross primary production, plant
32 optimality, ecosystem modelling

33 **Highlights**

- 34 • Building an evapotranspiration estimation framework based on *a priori* primary productivity model (the
35 P model).
- 36 • Assessing the contribution of environmental indicators to the ratio of transpiration to
37 evapotranspiration.
- 38 • Proving the reliability of this approach to estimate evapotranspiration.

39 **1. Introduction**

40 Evapotranspiration (ET) is a key process in the global terrestrial water cycle (Bai and Liu, 2018). ET
41 comprises the biotic process of transpiration (T) via stomata, and the abiotic processes of evaporation from
42 wet leaves (interception) and bare soil. ET is a core object for regional water management (Bastiaanssen et
43 al., 2000; Zeng et al., 2019) and the mitigation of excessive water consumption (Fisher et al., 2017). It
44 mediates energy exchange at the land-atmosphere interface and thereby influences regional and global
45 climate (Trenberth et al., 2009). Transpiration can indicate the growth status of both natural and cultivated
46 vegetation canopies due to the close coupling between carbon uptake and water transpired (Ershadi et al.,
47 2014). Accurate modelling and monitoring of ET are thus important for multiple applications in ecology,
48 hydrology and climate science.

49 Many ET models depend on remote sensing inputs (Mu et al., 2007, Wu et al., 2012). Apart from
50 empirical relationships employed in early studies (Moran et al., 1994, Nagler et al., 2013) and more recent

51 machine-learning approaches (Jung et al., 2009, Torres et al., 2011, Elnashar et al., 2021), ET is generally
52 predicted based on the land-surface energy balance. A conventional approach is to calculate the latent heat
53 flux representing the energy flux during the vaporization of water as the residual of the surface energy
54 balance equation (Bastiaanssen et al., 1998; Su, 2002; Norman et al., 1995). Sensible heat flux is commonly
55 predicted based on its relationship with the temperature gradient between the atmosphere at reference height
56 and the land surface, which can be simulated using remotely observed land surface temperature (LST)
57 (Lagouarde et al., 1991). However, remotely sensed signals suffer from extensive cloud contamination. Due
58 to the extreme sensitivity of sensible heat flux to LST, and LST to instantaneous climate conditions, the
59 robustness of monitoring time-series ET by this strategy may be compromised by input data quality (Tan et
60 al., 2019).

61 The Penman-Monteith (PM) equation provides an alternative, more direct approach to estimate the
62 latent heat flux and ET. This equation has also been applied widely to calculate ET (Granger et al., 1989;
63 Carlson et al., 1991; Allen et al., 1998; Cleugh et al., 2007; Mu et al., 2007; Leuning et al., 2008). Its
64 application depends on specifying surface conductance. Jarvis (1976) suggested that surface conductance
65 could be represented for different land-cover types by combining its empirical responses to meteorological
66 variables including air temperature, downward shortwave radiation, and soil moisture. This approach has
67 been applied globally (Mu et al., 2007, Zhang et al., 2019). However, ‘Jarvis-type’ modelling of surface
68 conductance entails substantial uncertainties because of the need to calibrate multiple parameters for
69 different land cover types.

70 Modern approaches to estimating surface conductance and ET in Earth System models (ESMs) rely on
71 the intrinsic coupling between photosynthesis and transpiration, both regulated by stomata (Wong et al.,
72 1979). Ball and Berry (1987) proposed an empirical model of stomatal conductance as a function of
73 photosynthesis and relative humidity (RH). Leuning (1995) developed this idea further, noting that vapour
74 pressure deficit (VPD) rather than RH is the driving force of ET (Leuning et al., 2008). These models have
75 been applied widely at a global scale (Kowalczyk et al., 2006, Oleson et al., 2010; Jiang et al., 2016; He et
76 al., 2018; Zhang et al., 2019). Medlyn et al. (2011) introduced a new stomatal conductance model based on
77 the Cowan and Farquhar (1977) hypothesis on optimal stomatal behavior. This new model has features in
78 common with the empirical models of Ball and Berry (1987) and Leuning (1995), and provides a partial
79 theoretical basis for them. However, all these models require the calibration of parameters that vary

30 substantially among biomes and regions (Lin et al., 2015; Knauer et al., 2018) and an assumption of their
31 constancy under changing environmental conditions. The multiplicity of poorly known parameters,
32 combined with the questionable assumption that they are constant, is likely to limit the usefulness of current
33 ET models for climate-change applications (Yang et al., 2019). Moreover, current ESMs show a pervasive
34 bias, systematically underestimating the importance of transpiration – to a greater or lesser extent in
35 different models – due to systematic errors in model representations of light absorption in plant canopies
36 (Lian et al., 2018).

37 It would be highly desirable, therefore, to develop universal models of photosynthesis and stomatal
38 conductance, applicable across biomes without re-calibration. A recently developed model for gross primary
39 production (GPP) (the P model: Wang et al., 2017, Stocker et al., 2020) provides such a way to avoid the
40 limitations of current models. At the core of the P model is a description of optimal stomatal behaviour as a
41 function of environment that is equally applicable to all C₃ plants (Prentice et al., 2014). The P model has
42 been used to diagnose the response of the terrestrial carbon cycle to changes in climate and atmospheric CO₂
43 (e.g. Keenan et al. 2016; Stocker et al., 2020); as part of a global monitoring system for GPP
44 (<https://terra-p.vito.be>); and as the basis for a generic scheme to predict wheat yields (Qiao et al., 2020).
45 Pérez-Priego et al. (2018) combined the P model and an empirical canopy conductance model to partition
46 observed ET into transpiration and evaporation, suggesting the potential to employ the P model globally to
47 estimate the transpiration component of ET.

48 Here we propose a modelling framework for ET based on the PM equation and the P model's estimation
49 of canopy conductance. This framework combines optimality theory with remote sensing data. We use
50 site-level observations to evaluate the model.

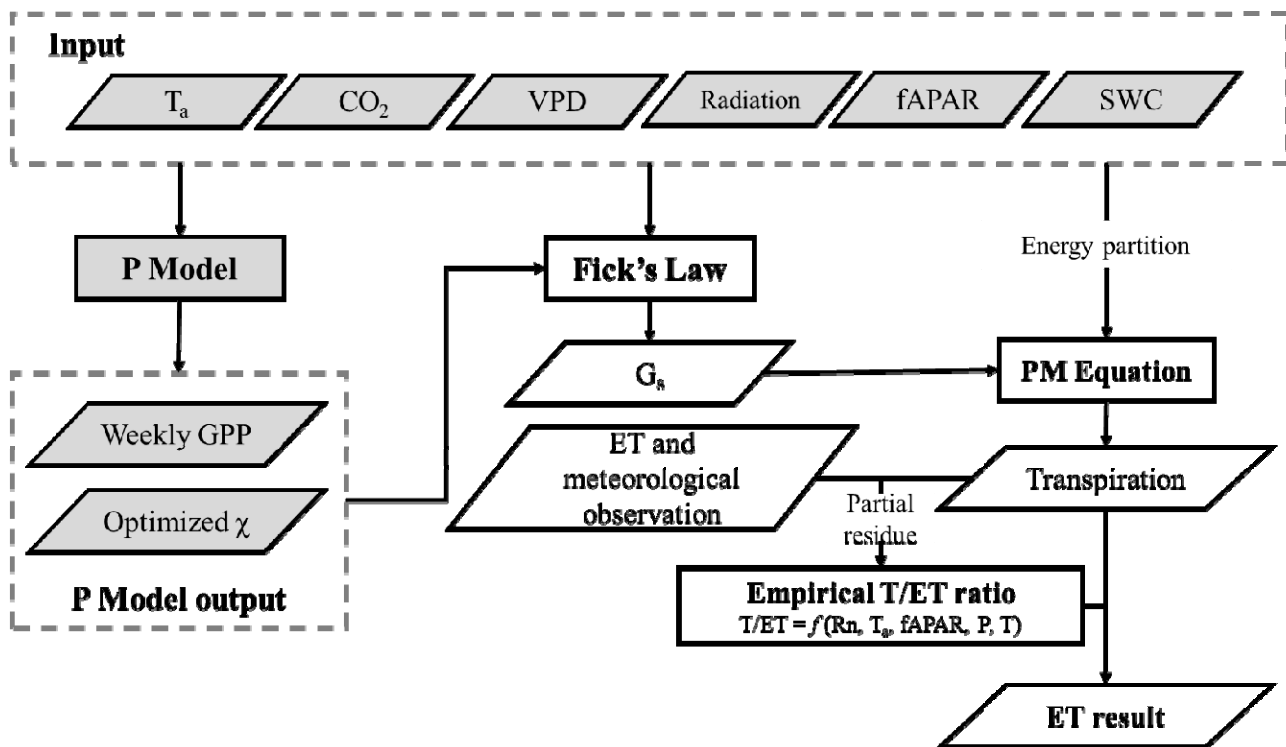
51 ***2 Materials and methods***

52 *2.1 A general framework for modelling ET*

53 The central operation in our proposed ET modelling framework is the estimation of canopy conductance,
54 based on GPP and the ratio of leaf-internal to ambient CO₂ partial pressure (c_i/c_a , denoted by χ), both of
55 which are calculated by P model. This calculation is independent of plant functional types, except for the
56 necessary distinction between C₃ and C₄ plants. The predicted GPP and χ values are used to estimate canopy

37 conductance to CO₂, which is multiplied by 1.6 to yield the estimated average canopy conductance to water
 38 vapour (G_s , mol m⁻² s⁻¹). We then estimate T with the PM equation driven by the predicted canopy
 39 conductance and meteorological variables. A weekly time step is adopted for the prediction of GPP, T and
 40 ET because the theory behind the P model is based on leaf-level acclimation of photosynthetic parameters to
 41 environment, which occurs over a time scale of weeks.

42 The ratio T/ET is constrained by local environment due to water limitation under dry conditions and
 43 energy limitation under wet conditions. There is evidence that this ratio is temporally conservative without
 44 disturbance on the local environment (Paschalis et al. 2018), perhaps because local wetness condition
 45 simultaneously controls transpiration and soil evaporation. Here, accordingly, we calculate site-specific (but
 46 time-invariant) values of T/ET from the predicted T and observed ET, allowing us both to test our
 47 simulations of the seasonal cycle of ET and to explore the potential environmental dependencies of this ratio
 48 (Fig. 1).



19
 20 **Fig. 1. Flowchart of the P model based ET prediction.** Items in grey have been validated by previous
 21 P model studies, summarized in Section 2.1.1. “Radiation” in the input block includes the four components
 22 of net radiation (R_n), and PPFD (photosynthetic photon flux density). SWC is the volumetric soil water
 23 content, which is an input to the P model. Canopy conductance is calculated by Fick’s law, which requires

24 simulated weekly GPP and χ (ratio of c_i/c_a) as input. The ratio T/ET is required for calculating ET from
25 modelled transpiration, and is fitted by ET and meteorological observation. In the empirical function, T_a is
26 air temperature in °C, fAPAR is the fraction of absorbed photosynthetically active radiation, and P is annual
27 precipitation in mm.

28 2.1.1 Predicting GPP and χ using the P model

29 The P model is an extension of the FvCB biochemical model of C₃ photosynthesis (Farquhar et al., 1980)
30 to account for optimal acclimation of photosynthetic capacities and stomatal behaviour (Wang et al., 2017,
31 Stocker et al., 2020: the reader is referred to these publications for the detailed equations and their
32 derivation). The instantaneous rate of photosynthesis according to the FvCB model is the lesser of the
33 electron transport-limited rate (A_J) and the carboxylation-limited rate (A_C). Both rates are limited by c_i , and
34 therefore depend on the product of c_a and χ . Based on the concept of eco-evolutionary optimality (Franklin
35 et al., 2020), the *least-cost hypothesis* states that plants minimize the total costs of maintaining carboxylation
36 capacity and transpiration through the regulation of stomatal conductance (Wright et al., 2003; Prentice et al.,
37 2014). This hypothesis leads to a prediction of optimal χ as a function of VPD, temperature and elevation
38 (Prentice et al., 2014; Wang et al., 2017).

39 A second optimality hypothesis, the *coordination hypothesis*, states that on a weekly to monthly time
40 scale, A_J and A_C converge (Chen et al. 1993; Haxeltine and Prentice 1996; Maire et al., 2012) by acclimation
41 of the maximum rate of carboxylation (V_{cmax}) (Smith et al., 2019). The maximum rate of electron transport
42 (J_{max}) is observed to vary in parallel to V_{cmax} . Optimal J_{max} is assumed to maximize the difference between
43 the benefit (A_J) and cost of maintaining a certain level of J_{max} (Wang et al., 2017; Smith et al., 2019). Wang
44 et al. (2017) showed that the least-cost and coordination hypotheses, together with this principle for the
45 optimization of J_{max} , lead to a closed-form expression for GPP. Despite its basis in the FvCB model of
46 instantaneous photosynthesis (which implies a non-linear, saturating response to light), this model has the
47 mathematical form of a light use efficiency (LUE) model: in other words, accumulated GPP for C3 plant
48 over the acclimation time scale is proportional to accumulated absorbed photosynthetic photon flux density
49 (PPFD). V_{cmax} and J_{max} do not have to be specified, because their optimal values are implicitly calculated by
50 the model.

51 We modified the P model to predict C_4 as well as C_3 photosynthesis based on the theory by Collatz et al.,
52 (1992). Given that phosphoenolpyruvate carboxylase (the initial carboxylating enzyme in the C_4 pathway)
53 has a higher affinity for CO_2 than Rubisco (the primary carboxylating enzyme of the C_3 pathway), we
54 assumed that C_4 photosynthesis is not limited by the intercellular CO_2 concentration (Sayre et al., 1979). The
55 model as applied here also includes the generic soil-moisture limitation function described by Stocker et al.
56 (2020) and temperature dependencies of the intrinsic quantum efficiency of photosynthesis, based on
57 measurements by Bernacchi et al. (2003) for C_3 plants (Stoker et al., 2020) and Kubien et al. (2003) for C_4
58 plants (Cai & Prentice, 2020). The soil moisture function requires an estimate of a climatological aridity
59 index, which was calculated for each site using in-situ observation and the Priestley-Taylor equation
60 (Priestley and Taylor, 1972). The full model code is available at <https://github.com/stineb/rpmodel>.

31 *2.1.2 Canopy conductance*

32 The diffusion of both water vapour and CO_2 through stomata can be described by Fick's law. CO_2
33 diffusion into the leaf is driven by the difference between the ambient and leaf-internal concentrations. We
34 scale up from leaf to canopy level in the simplest possible way via the “big-leaf” approximation. Thus,
35 canopy stomatal conductance to water vapour is given by:

$$36 \quad G_s = 1.6 \frac{GPP}{c_a(1-\chi)} \quad (1)$$

37 where the factor 1.6 is the ratio of the molecular diffusivities of water and CO_2 . For C_4 plants, we set χ in
38 equation (1) to a typical value of 0.45 (Farquhar et al., 1989).

39 *2.1.3 Transpiration*

70 Total latent heat flux (λE_t) can then be decomposed into contributions from transpiration (λE_c) and
71 evaporation (λE):

$$72 \quad \lambda E_t = \lambda E_c + \lambda E \quad (2)$$

73 where λ is the latent heat of evaporation of water ($MJ \text{ kg}^{-1}$). λE_c was calculated using the
74 Penman-Monteith equation:

$$75 \quad \lambda E_c = \frac{\Delta Q_{n,c} + \rho c_p VPD g_a}{\Delta + \gamma(1 + g_a/G_s)} \quad (3)$$

76 where Δ is the slope of the curve relating saturation water vapour pressure to air temperature (kPa K^{-1}) and
77 $Q_{n,c}$ is the available energy (net radiation) intercepted by the canopy (W m^{-2}), i.e., a fraction of the total net
78 radiation minus soil heat flux ($R_n - G$). Because shortwave radiation is generally the largest part of net
79 radiation, this fraction was estimated by Beer's Law as $Q_{n,c}/Q_n = 1 - \exp(-k LAI)$, where k is the
30 extinction coefficient, assumed constant at 0.5. This has a similar mathematical form to the calculation of
31 fAPAR from LAI (leaf area index) (Gan et al., 2018; Zhang et al., 2019). ρ in equation (3) is the density of
32 air (kg m^{-3}), c_p is the heat capacity of dry air ($\text{J kg}^{-1} \text{K}^{-1}$), G_s is calculated by equation (1), and g_a is the
33 aerodynamic conductance calculated by the simple model of Thom (1972):

$$34 \quad 1/g_a = \frac{u}{u_*^2} + 135u_*^{-0.67} \quad (4)$$

35 where u is the wind speed (m s^{-1}) and u_* (m s^{-1}) is the friction velocity, which is obtained from flux
36 observations. The even simpler equation recommended by FAO (Allen et al., 1998) was used when no
37 information on u_* was available:

$$38 \quad 1/g_a = 208/u \quad (5)$$

39 *2.1.4 Site-specific ratio of transpiration to total evapotranspiration*

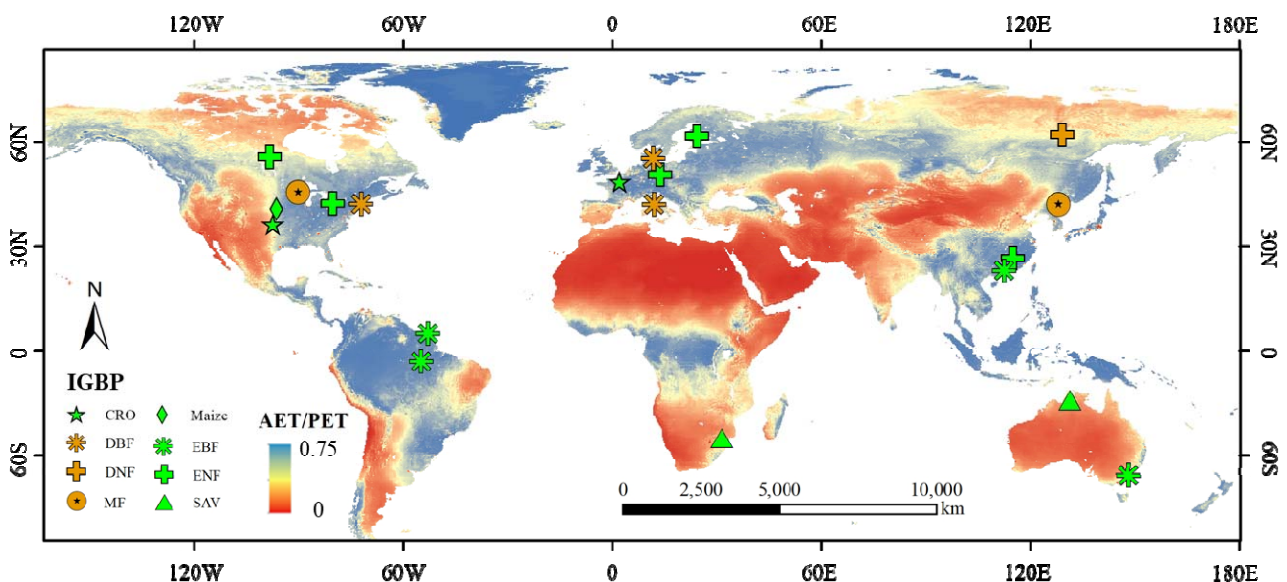
40 Fatichi et al. (2017) used a detailed, mechanistic ecosystem model that simultaneously solves for water,
31 energy, and carbon exchanges over the land surface to analyse global variation in simulated T/ET. Their
32 results suggested that T/ET is globally constrained to $70 \pm 9\%$ with only modest effects of climate or
33 vegetation type – although under some extreme conditions, such as drip-irrigated farmland, the ratio could
34 lie outside this range (Kool et al., 2014). Here we assumed a constant T/ET ratio at each site, and estimated
35 this ratio using a priori relationship between modelled transpiration as described above (equations 1–5) and
36 the observed ET and meteorological conditions.

37 We then estimated partial effects (effects of each predictor variable with the others held constant at their
38 median values) in a multiple regression to analyse how T/ET ratio varies with environment. Five indicators
39 (R_n , fAPAR, T_a , P , and modelled transpiration) were selected as potential predictors. The first four of these
40 indicators are the inputs to the empirical soil evaporation model of Zhang et al. (2010). Transpiration was

31 selected to describe the contribution of environmental water supply, since soil water content information is
32 not available at all flux sites.

33 2.2 Sites and in situ observations

34 Twenty sites with 228 observation-years of flux data (including sensible heat flux, latent heat flux and
35 soil heat flux) from the FLUXNET2015 Tier 1 data (<https://fluxnet.fluxdata.org>) were used. We employed a
36 site selection criterion that the energy balance ratio $(R_n - G)/(R_n + H)$ must lie between 0.8 to 1.2 (where
37 H represents sensible heat flux). These sites span eight main land cover types (Table 1, Fig. 2). Weekly
38 measurements of T_a , wind speed, the four components of radiation (downward and upward long-wave and
39 short-wave radiation), soil water content and ambient CO_2 concentration are recorded at all these sites, and
40 were used to drive the P model. Daily ecosystem carbon exchange was partitioned into GPP and ecosystem
41 respiration using the half-hourly night-time separation method of Reichstein et al. (2005). Unreliable records
42 were filtered out before weekly averaging by imposing the following requirements: (1) available energy (net
43 radiation minus soil heat flux) > 0 , which is a pre-requisite for evapotranspiration; (2) average air
44 temperature $> 5^\circ\text{C}$ and GPP > 0 ; (3) precipitation = 0; (4) LAI > 0 ; (5) less than 10% fAPAR is ineffective in
45 the focused year (e.g. GF-Guy in 2014 was heavily contaminated by cloud).



16

17 **Fig. 2. Map of flux sites.** Twenty sites from eight major biomes, according to the International
18 Geosphere-Biosphere Programme (IGBP) classification. **CRO** = crop, **DBF** = deciduous broadleaf forests,

19 **DNF** = deciduous needleleaf forests, **MF** = mixed forests, **EBF** = evergreen broadleaf forests, **ENF** =
20 evergreen needleleaf forests, **SAV** = savanna, **MAI** = maize. The map background is averaged ratio of mean
21 ratio of actual evapotranspiration (AET) dividing potential evapotranspiration (PET) through the year of
22 1990 to 2015 from GLDAS (Global Land Data Assimilation System, v2.1) (Rodell et al., 2004).

3 **Table 1.** Information on the selected flux sites. **Lon** = longitude (°), **Lat** = latitude (°), **Ele** = elevation (m). **MAT** = mean annual temperature (°C), **MAP** =
 4 mean annual precipitation (mm). Biome type codes are the same as in Fig. 2.

D	Site Name	L on	L at	E le	I GBP	Data Range	M AT	M AP
	AU-D	13	-1	4	S	2008-2	2	9
	as	1.39	4.16	70	AV	014	7.2	76
	AU-T	14	-3	1	E	2001-2	1	1
	um	8.15	5.66	200	BF	014	0.7	159
	BR-S	-5	-3	1	E	2000-2	2	2
	a3	4.97	.02	00	BF	004	6.1	043
	CA-M	-9	5	2	E	1994-2	-	5
	an	8.48	5.88	59	NF	008	3.2	20
	CA-T	-8	4	1	E	2009-2		1
	p3	0.35	2.71	84	NF	014	8	036
	CN-C	12	4	7	M	2003-2	2	6
	ha	8.1	2.4	66	F	005	.2	64
	CN-D	11	2	3	E	2003-2	1	1
	in	2.54	3.17	08	BF	005	9.6	618
	CN-Q	11	2	1	E	2003-2	1	1
	ia	5.06	6.74	09	NF	005	9	467
	DE-T	13	5	3	E	1996-2	8	8
	ha	.57	0.96	85	NF	014	.2	43
0	DK-S	11	5	4	D	1996-2	8	6
	or	.64	5.49	0	BF	014	.2	60
1	FI-Hy	24	6	1	E	1996-2	3	7
	y	.29	1.85	81	NF	014	.8	09
	FR-Gr	1.	4	1	C	2004-2	1	6

2	i	95	8.84	25	RO	014	2	50
	GF-G	-5	5.	4	E	2004-2	2	3
3	uy	2.92	28	8	BF	014	5.7	041
	IT-Ro	11	4	1	D	2002-2	1	8
4	2	.92	2.39	60	BF	012	5.2	76
	RU-S	12	6	2	D	2012-2	-	2
5	kp	9.17	2.26	46	NF	014	1.1	90
	US-A	-9	3	3	C	2003-2	1	8
6	rm	7.49	6.61	14	RO	012	4.8	43
	US-H	-7	4	3	D	1991-2	6	1
7	a1	2.17	2.54	40	BF	012	.6	071
	US-N	-9	4	3	M	2001-2	1	7
8	e1	6.48	1.17	61	AI	013	0.1	90
	US-P	-9	4	4	M	1995-2	4	8
9	Fa	0.27	5.95	72	F	014	.3	23
	ZA-K	31	-2	3	S	2000-2	2	5
0	ru	.5	5.02	59	AV	013	1.9	47

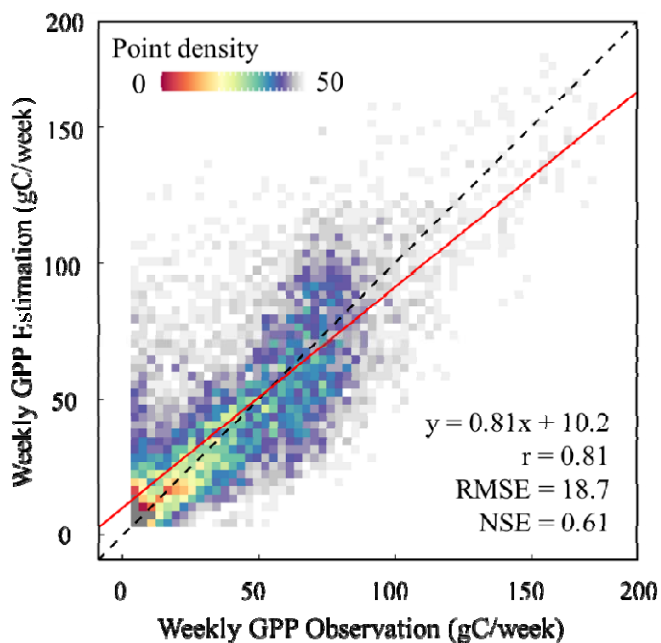
25 2.3 Remote sensing observations

26 Remotely sensed fAPAR is required as an input by the P model. Since some of the flux records started
27 in the early 1990s, we used the fAPAR product from NOAA CDR AVHRR with a 0.05° spatial resolution in
28 order to maintain consistency of the model input (Claverie and Vermote, 2014). fAPAR time series were
29 smoothed by a Savitzky–Golay filter to eliminate high-frequency noise (Chen et al., 2004).

30 3 Results

31 3.1 Predicting weekly GPP using the P model

32 Weekly predicted GPP was well supported by observations (Fig. 3 and Table 2). The correlation
33 coefficient (r) based on all records was 0.81, the RMSE (root mean squared error) is 18.7 gC/week, and the
34 NSE (Nash-Sutcliffe efficiency coefficient) is 0.61. At site scale, r ranged from 0.48 (at BR-Sa3) to 0.92 (at
35 CN-Cha), and RMSE from 6.2 gC/week (at RU-Skp) to 24.8 gC/week (at US-Ne1). This good performance
36 is consistent with previous P model evaluation studies (Wang et al., 2017; Stocker et al., 2018, 2020; Qiao et
37 al., 2020). The good performance at the maize site (US-Ne1) supports its extension to C_4 vegetation (RMSE
38 = 24.8 gC/week, and a 24.5% of relative root mean squared error, denoted as RRMSE). The model tends to
39 slightly underestimate GPP (fitting slope is 0.81); this bias can be removed by calibrating a single, global
40 parameter representing the efficacy with which absorbed light is used in photosynthesis (Stocker et al.,
41 2020), but we did not apply any such *a posteriori* adjustment. The underestimation is probably due at least
42 in part to mismatches of the flux tower footprints with the AVHRR fAPAR grids (Kljun et al., 2015).
43 Heterogeneity inside the target RS pixel ($0.05^\circ \times 0.05^\circ$), but not in the tower footprint, especially patches of
44 bare soil, would be expected to reduce the measured fAPAR by increasing reflectance in the red band,
45 leading to an underestimation of absorbed radiation.



16

17 **Fig. 3. Comparison of estimated GPP against observations at a weekly time scale.** The red line is
 18 the linear fit; the dashed line is the 1:1 line. Colours represents the density of points.

19 **Table 2. Statistical information on the GPP evaluations on a weekly timestep.** Slope: coefficients of
 20 linear fits, r : correlations between observed and predicted values, RMSE: root mean squared error of
 21 prediction, RRMSE: relative root mean squared error.

Site Name	GPP estimation result		
	r	RMSE (g C/week)	RRMSE (%)
AU-Das	0.75	7.4	23.5
AU-Tum	0.59	16.1	26.6
BR-Sa3	0.48	15.8	25.0
CA-Man	0.77	10.3	34.7
CA-TP3	0.61	20.3	44.1
CN-Cha	0.92	9.2	16.4
CN-Din	0.78	7.8	25.0
CN-Qia	0.87	8.2	21.6
DE-Tha	0.75	14.6	28.4
DK-Sor	0.89	16.1	24.2
FI-Hyy	0.89	11.7	27.4
FR-Gri	0.61	25.3	34.4
GF-Guy	0.49	24.1	33.3
IT-Ro2	0.63	16.9	34.9
RU-Skp	0.82	6.2	24.6
US-Arm	0.68	7.7	22.8
US-Ha1	0.84	19.3	33.0

US-Ne1	0.86	24.8	24.5
US-PFa	0.88	8.5	20.7
ZA-Kru	0.65	9.3	24.2

52 3.2 Estimating T/ET ratio

53 The fitted slope in Table 3 indicates that the ratio T/ET ranged from 0.52 (FR-Gri) to 0.92 (CA-Man).
 54 The five selected predictors of this ratio (net radiation, fAPAR, precipitation, air temperature and modelled
 55 transpiration) all contributed significantly to determine T/ET ($p < 0.05$; see Fig. 4). T/ET increased with net
 56 radiation, precipitation and fAPAR and decreased with air temperature and transpiration. According to the
 57 theory of Zhang et al. (2010), higher fAPAR leads to greater energy interception by the canopy and therefore
 58 a higher T/ET. More energy (higher R_n and T_a) and precipitation should, all else equal, lead to a denser
 59 canopy and thus larger fAPAR. But increasing temperature increases soil evaporation more than
 60 transpiration. The net effect of T_a on T/ET ratio is therefore negative (Fig. 4d). As T increases, T/ET
 61 decreases. This negative effect (Fig. 4e) suggests that soil evaporation is more sensitive to changing energy
 62 inputs, due to the limitation of transpiration by stomata.

63 We estimated T/ET ratio at site level using the empirical relationship between the T/ET and the five
 64 variables using the following relationship:

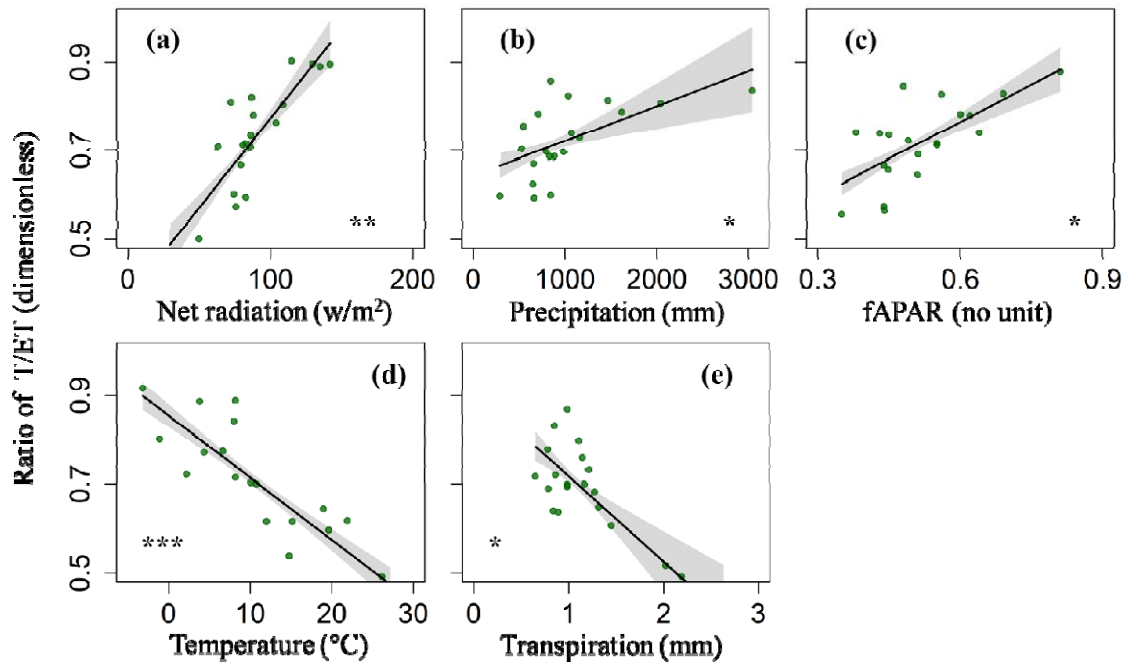
$$65 \quad T/ET = 4.05 \times 10^{-3}R_n + 7.94 \times 10^{-5}P + 0.56 \times fAPAR - 0.0014 \times T_a - 0.19 \times T + 0.37 \quad (6)$$

66 The correlation coefficient of the model against fitted (linear regressed by modelled T against ET
 67 observation) T/ET ratio was 0.84 based on site-average conditions (see Fig. 5). Analysis of the dependencies
 68 of this estimated ratio on several predictor variables suggested that denser canopies significantly lead to
 69 higher values of T/ET, as also suggested by Wang et al. (2014). Results of cross-validation (at each target
 70 site re-fitting the relationship using data from other sites, then using the new function to estimate ET at the
 71 target site, see Fig. S1) indicate the robustness and reliability of this approach at different sites.

72 **Table 3. Statistical information on the ET evaluations on a weekly timestep.** Slope in table
 73 represents linear fitting slope of estimated transpiration to ET observation, which is considered as the T/ET
 74 ratio. Other items have the same meaning with its in Table 2.

Site Name	ET estimation result		
	Slope	r	RRMSE (%)

AU-Das	0.56	0.8 2	4.4	29.5
AU-Tum	0.81	0.8 1	5.7	21.5
BR-Sa3	0.62	0.8 5	2.5	9.9
CA-Man	0.92	0.8 9	4.3	41.3
CA-TP3	0.78	0.7 3	4.7	28.1
CN-Cha	0.67	0.9 5	2.7	18.6
CN-Din	0.68	0.8 4	4.8	39.9
CN-Qia	0.65	0.9 0	4.9	36.7
DE-Tha	0.84	0.7 4	5.3	41.3
DK-Sor	0.52	0.8 7	3.7	23.3
FI-Hyy	0.86	0.8 8	3.9	29.3
FR-Gri	0.52	0.8 2	4.4	32.8
GF-Guy	0.62	0.5 1	4.8	16.6
IT-Ro2	0.74	0.8 7	5.4	41.8
RU-Skp	0.71	0.6 6	4.1	36.0
US-Arm	0.54	0.7 1	4.8	42.8
US-Ha1	0.84	0.8 5	5.7	37.2
US-Ne1	0.62	0.9 1	5.0	26.1
US-PFa	0.79	0.9 3	3.1	22.7
ZA-Kru	0.68	0.7 7	5.5	38.8



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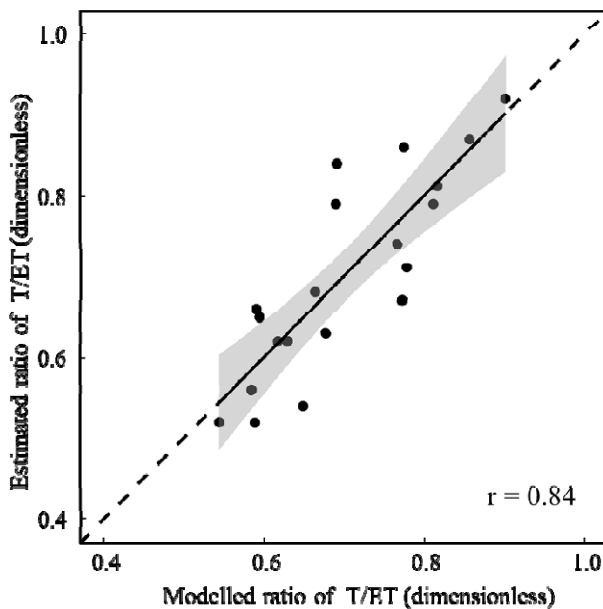
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Fig. 4. Partial residual plots from the regression of site-scale transpiration to evapotranspiration ratio (T/ET) against environmental predictors. Net radiation, fAPAR, air temperature and modelled transpiration are averaged by effective observation during growing season at each site, except precipitation (mm) in (b) which is an annual accumulated total. Radiation (W/m^2) in (a) represents net radiation. Grey colours in all panels represents 95% confidence intervals. Significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

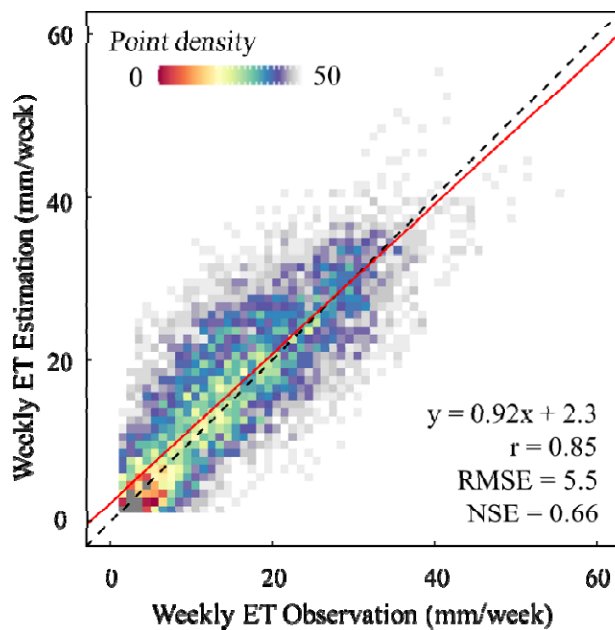


33

34 **Fig. 5. Comparison of predicted and modelled (linear regressed by modelled T against ET**
35 **observation) T/ET ratio at each flux sites.** The predictions are based on the empirical environmental
36 dependences. Grey colour represents 95% confidence intervals; the dashed line is the 1:1 line.

37 3.3 Performance of ET estimation

38 We obtained a good validation result of modelled ET against flux observations (slope = 0.92, $r = 0.85$,
39 RMSE = 5.46 mm week⁻¹ and NSE = 0.66, see Fig. 6). Good performance of the model was also shown by
30 correlation at site level (r ranges from 0.51 to 0.95), and RMSE (from 2.50 to 5.71 mm week⁻¹).



31

32 **Fig. 6. Comparison of estimated ET using the approach in this study against observation with**
33 **weekly time scale.** The red line is the linear fit; the dashed line is the 1:1 line. Colours represents the density
34 of points.

35 4 Discussion

36 We have demonstrated an approach to estimate evapotranspiration that greatly reduces the need to
37 specify uncertain parameters. It points the way towards a parsimonious general theory of ET estimation from
38 remotely sensed observations and environmental variables. The improvement also avoids discontinuities due

39 to the need to impose biome boundaries when biome-specific parameters are required. This approach, based
40 in part on optimality theory, could provide a means to improve the monitoring and forecasting of ET.

41 *4.1 Success of the a priori method*

42 In our framework, GPP and ET are estimated without the need to estimate or calibrate biome or plant
43 functional type specific parameters. The imposition of biome boundaries, required by many existing
44 methods, creates uncertainty for two reasons. First is the quality of terrestrial classification. Remotely sensed
45 classification maps always have reasonable accuracy for types with clear spatial or temporal pattern, but
46 there are still uncertainties, especially in wet regions with major cloud contamination (Zhang et al., 2018).
47 Incorrect biome identification would influence the parameters and thus the results (see the example Fig. S2).
48 In addition, separate parameter fitting by biomes can obscure systematic differences among modelled
49 responses to environment (see Fig. S3). The P model, in contrast, is based on a universal plant optimality
50 theory that implicitly predicts differences among biomes as a consequence of the environments where they
51 occur.

12 *4.2 Uncertainties*

13 The P model provides a universal strategy to calculate canopy conductance in C₃ vegetation and is
14 extended to C₄ plants in a straightforward way. The good results at the maize site US-Ne1 support this
15 approach. The current version however adopts a constant value of 0.45 for χ in C₄ plants (Farquhar et al.,
16 1989), a simplification that could be improved on.

17 The conversion from transpiration to total evapotranspiration is based on a T/ET ratio, which was
18 considered as a constant at each site. In Fig. S4, we tested this assumption by constructing a global map of
19 the standard deviation of the annual T/ET ratio in the PMLv2 (Penman-Monteith-Leuning) data set from
20 2003 to 2017 (Zhang et al., 2019). PML was chosen because its strategy for partitioning available energy in
21 the PM equation is the same as the one we used. Most of the region (nearly 80%) has a T/ET standard
22 deviation < 0.05 over these 15 years. Less than 1% of the area has a standard deviation > 0.1. In addition,
23 since the energy intercepted by canopy is calculated by fAPAR, area with significant variation of T/ET are
24 mainly located in the region with a significant variation in terrestrial LAI, both greening and browning, as
25 shown by Zhu et al., (2016).

26 A comparison with global patterns in other global T/ET products, including PML and GLEAM, shows
27 that the three remote-sensing based T/ET estimates yield similar latitudinal profiles (see Fig. S5). However,
28 the averaged value in PML (0.46) is substantially lower than in GLEAM (0.62) and our empirical method
29 (0.68). In regions with extremely sparse vegetation, such as North Africa and the Tibetan plateau (about 0.3
30 by our method, compared with near-zero in GLEAM and no value given in PML), we overestimated T/ET.
31 There are two possible reasons for this. First, fAPAR has a paramount contribution to our prediction, which
32 responds to the low fAPAR in such regions. Second, we employed only 20 sites during the fitting, and none
33 of them were from arid regions, so there is a possibility of bias.

34 Comparisons in this study (Fig. S6) and Gu et al., (2018) point to large difference between products and
35 estimation strategies for T/ET. Large differences have also been reported in ESMs (Lian et al., 2018). We
36 hope to improve the performance and temporal resolution of T/ET modelling with the help of multiple
37 observation strategies in near future. Possible more explicitly process-based approaches to modelling the
38 non-T components of ET include the flux variance similarity (FVS) partitioning method proposed by
39 Scanlon and Sahu (2008), and the use of data from lysimeters and sap flow meters (Zhou et al., 2018,
40 Nelson et al., 2020).

41 The scientific advance presented here lends itself naturally to application with remote sensing
42 technology. The only satellite-derived input is fAPAR, here at 5 km spatial resolution – but this implies a
43 mismatch with the flux tower footprints that may explain the underestimation of GPP at some sites.
44 Although this underestimation is corrected automatically in the process of estimating T/ET ratios, it would
45 be desirable to reduce it by using remotely sensed input with finer spatial resolution, such as images from
46 MODIS (MOderate Resolution Imaging Spectroradiometer), to better fit the tower footprint. There is also
47 the potential to improve the accuracy of fAPAR estimation from satellites. For example, according to Zhang
48 et al. (2020), light absorbed by chlorophyll (Chl) should provide a better basis for the estimation of GPP; a
49 variety of indices that more accurately represent Chl absorption are becoming available. Moreover, ET could
50 usefully be mapped with, say, 30 m or finer spatial resolution, as climate variables tend to vary much more
51 smoothly than vegetation properties (Tan et al., 2019). An improved, high-resolution satellite-based ET
52 estimation strategy would have many applications in land-surface modelling and water resources research.

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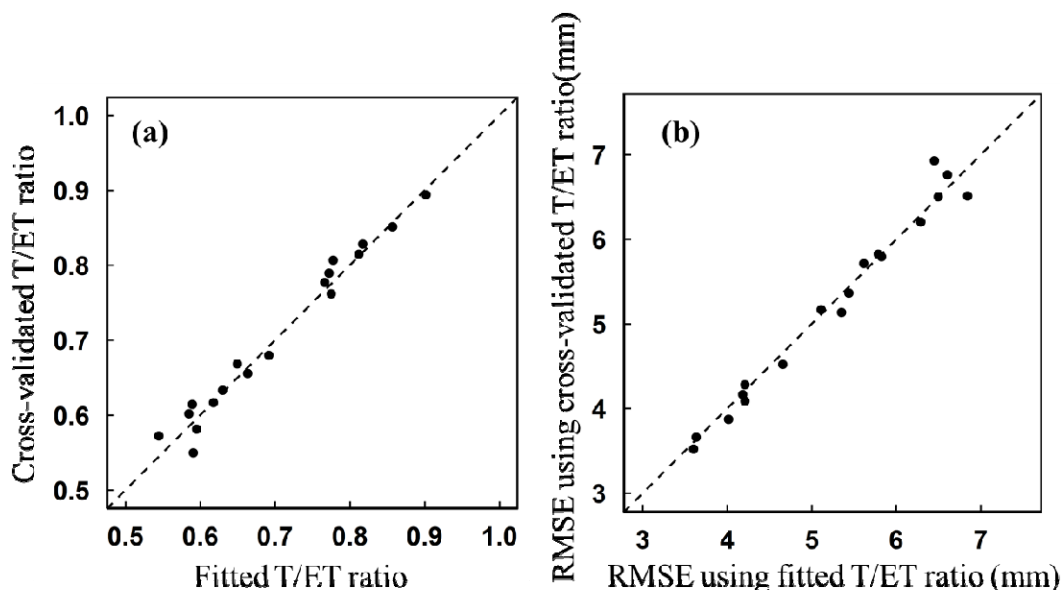
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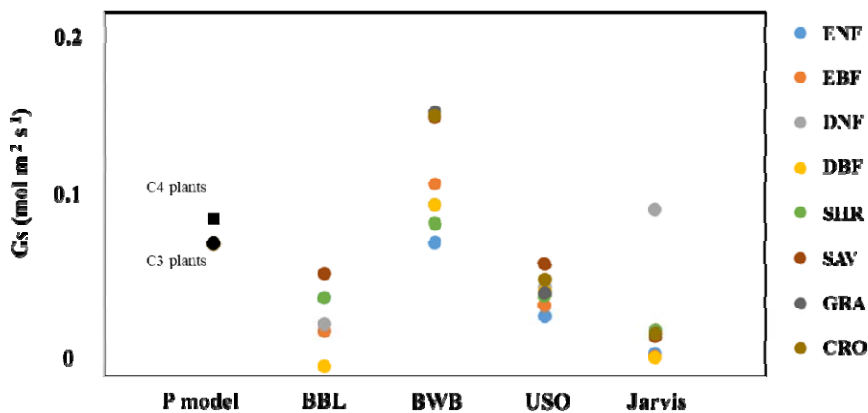
50 **Supplementary Information**



51

52 **Fig. S1. Cross-validation of the T/ET fitting theory.** X-axis is fitted T/ET ratio (in panel a) and RMSE
 53 of ET result (in panel b) using the universal function. Y-axis is T/ET ratio (in panel a) and RMSE of ET
 54 result (in panel b) result using the cross-validated function (exempting each target site during fitting).

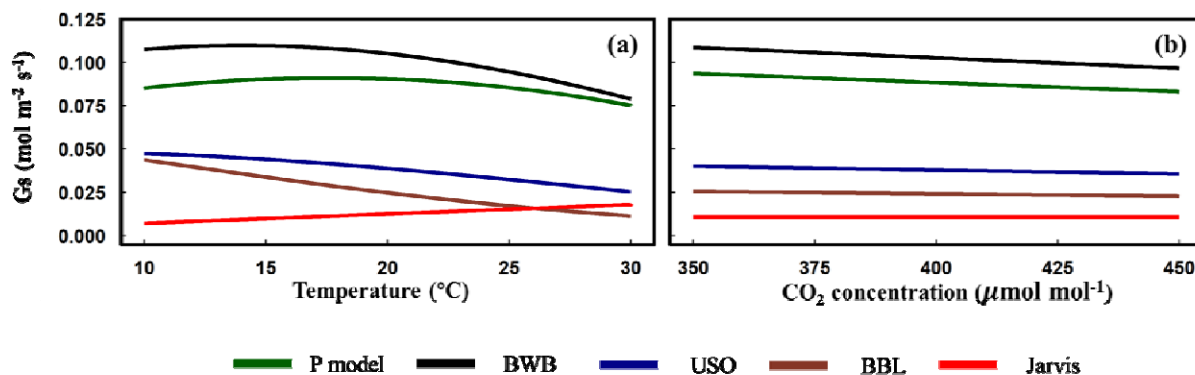
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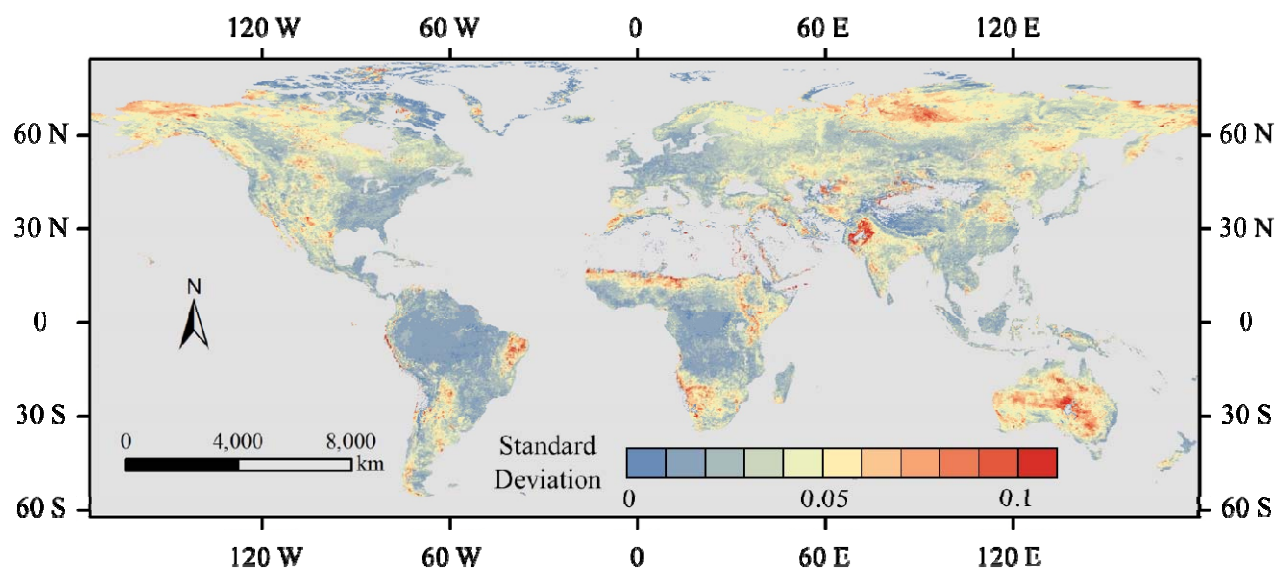
57 **Fig. S2. Comparison of typical conductance models under baseline condition** ($\rho_a=20$,
 58 $VPD=10\text{hPa}$, $fAPAR=0.8$, $\rho_a=380\ \mu\text{mol mol}^{-1}$, $SWC=0.2\ \text{m}^3\ \text{m}^{-3}$, $PPFD=275\ \mu\text{mol}^{-2}\ \text{photon s}^{-1}$). Two black
 59 points represents result estimated by C3 and C4 P model version respectively. Different colour represents

30 different biomes types. BBL represents Ball-Berry-Leuning conductance model (Leuning, 1995), BWB
31 represents Ball-Berry model (Ball and Berry, 1987), USO represents Mdelyn model (Medlyn et al., 2011),
32 Jarvis represents Jarvis model (Jarvis, 1976). For each conductance model requires GPP as input, we use the
33 result estimated by P model.



34

35 **Fig. S3. Comparison of typical conductance models response to increasing temperature and**
36 **ambient CO₂ concentration.** Baseline condition and model code is the same with Fig. S1.



37

38 **Fig. S4. Standard deviation map of PML T/ET ratio.** The calculation is based on the PML v2 product
39 from 2003 to 2017 (Zhang et al., 2019).

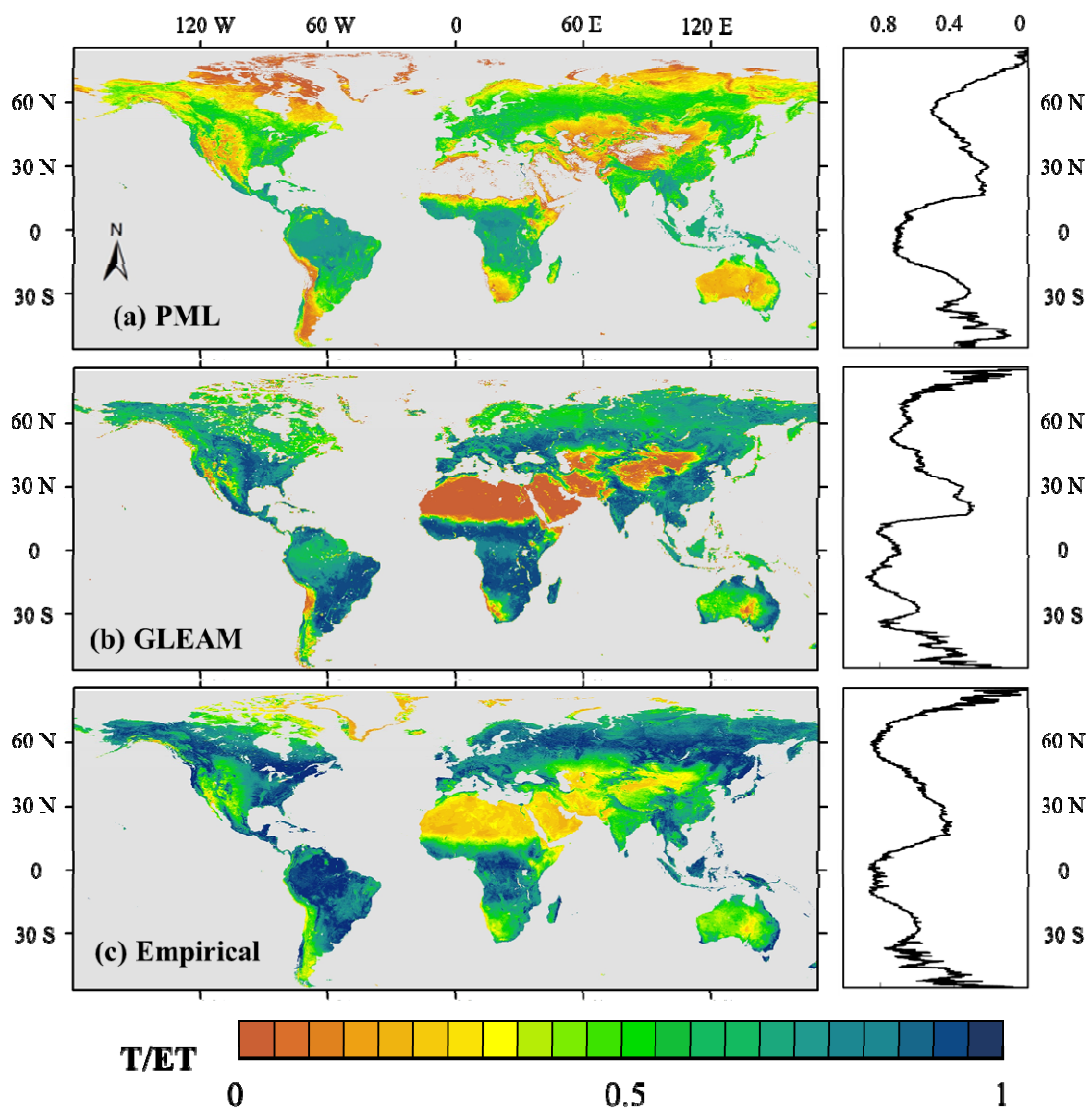
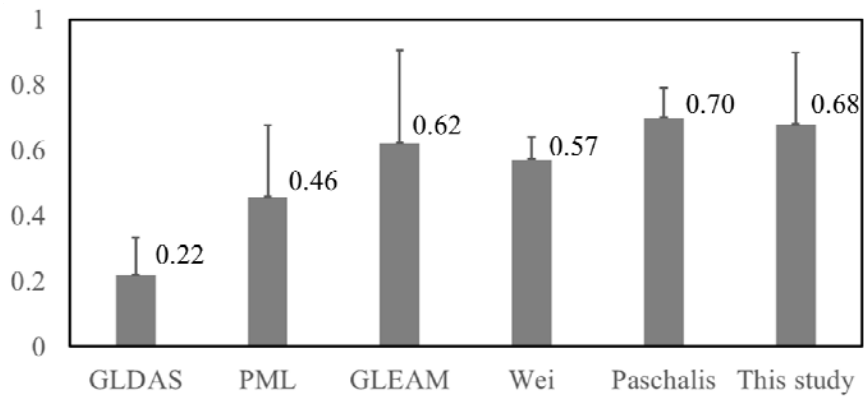


Fig. S5. Global distribution of T/ET ratio, provided by (a) PML, (b) GLEAM, and (c) the empirical method in this research. Latitude T/ET profile of each product is given next to each map. Data displayed here is an average between 2003 to 2017, during the period the PML product is available.



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Fig. S6. Summarized result of global T/ET ratio. Mean T/ET value is labelled next to each column.

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Standard deviation is represented by the error bar. Result of Wei was reported by Wei et al., (2017). Result of

77

Paschalis was reported by Paschalis et al., (2018). Global products (GLDAS v2.1, PML v2 and GLEAM

78

v3.3) are calculated based on data between 2003 to 2017.