



1 **A synthesis of water, energy, and carbon fluxes sensitivity to climate**
2 **variables in Southeast Asia**

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21 **Abstract**

22 Southeast Asia (SEA) plays an important role in the Earth's carbon and water cycle,
23 yet ecohydrology dynamics occurring in this region remain poorly understood due to
24 the paucity of field observations and modelling studies. Here, we investigate water,
25 energy, and carbon fluxes by combining existing flux tower data with mechanistic
26 ecohydrological modelling for 20 sites. A sensitivity analysis to meteorological
27 forcings is used to understand water and energy limitations. Results show large
28 latitudinal differences but overall suggest a strongly energy-limited region, where
29 evapotranspiration (ET) is tightly correlated with net radiation and is highly
30 responsive to relative humidity. Gross primary productivity (GPP) is also correlated to
31 net radiation and is most responsive to shortwave radiation changes. Only a few
32 ecosystems in SEA show signs of water limitations, such as certain grasslands in the
33 Tibetan plateau, savannas, and dry deciduous forests. We further disentangled the
34 relative effect of warming and humidity changes in vapor pressure deficit (VPD).
35 Sensitivity analysis indicates that climate warming-induced VPD changes – rather
36 than pure warming – can have important effects on ET but the opposite is true for
37 GPP with complex GPP responses to temperature based on the thermal photosynthetic
38 optimum and phenological responses. Water use efficiency (WUE) is highly
39 correlated with annual mean precipitation across space, but its responses to
40 precipitation changes are less consistent and WUE changes are most sensitive to
41 relative humidity. Carbon use efficiency (CUE) is more responsive to air temperature
42 than other climate drivers. These insights quantify water, energy, and carbon fluxes in
43 an underrepresented part of the Earth and enhance our understanding of how climate
44 can modify carbon and water cycles in this region.



45 **Key points**

- 46 • Ecosystems in Southeast Asia are mainly energy-limited, with a few
- 47 exceptions.
- 48 • ET in Southeast Asia is most sensitive to relative humidity changes rather than
- 49 purely air temperature, while GPP is most responsive to shortwave radiation.
- 50 • WUE is most sensitive to relative humidity and CUE is most responsive to air
- 51 temperature

52 **1 Introduction**

53 Southeast Asia (SEA) is characterized by a very distinct gradient in vegetation cover,
54 going from a dense equatorial forest in Indonesia and Malaysia up to cold-adapted
55 grasslands in the southern Tibetan Plateau (south of 34° N). With its high land-
56 atmosphere CO₂ fluxes, this region plays an important role in Earth's carbon (C) and
57 water cycles (Beer et al., 2010; Sullivan et al., 2020). Yet, the ecohydrology of SEA
58 has historically been understudied due to a combined paucity of field observations and
59 relatively few regional modelling efforts targeted to SEA. Therefore, only few articles
60 exist describing water, energy, and carbon fluxes of ecosystems across SEA
61 (Giambelluca et al., 2016; Huete et al., 2008; Kuricheva et al., 2021; Qian et al., 2019;
62 Song et al., 2017; Tan et al., 2012; Tanaka et al., 2008; Tang et al., 2018; Wang et al.,
63 2022; Zhang et al., 2016), with some broader synthesis for a few sites in Asia (Hirata
64 et al., 2008; Kato & Tang, 2008; Saigusa et al., 2008), but largely missing for the
65 entire SEA region. This hinders the effective evaluation of carbon and water fluxes
66 and prediction of future water availability in SEA (Sirisena et al., 2018; Vu et al.,
67 2023; Yuan Zhang et al., 2016). Furthermore, the expected increase of vapor pressure
68 deficit (Novick et al., 2024), the change in the frequency of extreme weather events,



69 and the shifts in precipitation patterns under climate change could pose a significant
70 threat to vegetation productivity and its capability to maintain carbon storage (Aadhar
71 & Mishra, 2020; Cervarich et al., 2016; Thirumalai et al., 2017), with SEA being
72 identified as one of the largest sources of uncertainties in the estimation of terrestrial
73 carbon sink (Bastos et al., 2020). It is therefore imperative to understand the
74 sensitivity of these ecosystems to climate variables.

75 SEA covers an area of approximately 7.5 million km² and features a broad climate
76 and vegetation gradient (Estoque et al., 2019; Qian et al., 2019). The majority of this
77 region is affected by a monsoon climate, characterized by two distinct wet and dry
78 seasons (Huete et al., 2008). The wet season of SEA – lasting from June to October
79 for north of the Equator and from November to February for south of the Equator –
80 receives substantial precipitation from the monsoon. On the other hand, the dry season
81 of SEA – extending from December to March for north of the Equator and from June
82 to September for south of the Equator – is marked by prolonged dry spells that
83 typically last more than a week (Wang, 2006). In this study we mostly focused on
84 regions North of the Equator because of data availability and because ~80% of SEA
85 land is located north of the Equator.

86 The distribution of natural vegetation in SEA is primarily shaped by elevation and
87 latitude (Figure 1). Regions near the Equator are predominantly covered by tropical
88 broadleaf evergreen rainforest, which receive a continuous supply of precipitation
89 with little seasonality (Estoque et al., 2019; Zhang et al., 2016). Large regions of
90 pristine tropical forest have, however, been converted into oil palm and rubber
91 plantations (Vijay et al., 2016; Wang et al., 2023). In contrast, as we move north, the
92 dry season becomes more pronounced, and land cover is characterized by a transition
93 between broadleaf evergreen forests and dry deciduous broadleaf forests in the



94 lowlands, while evergreen forests persist at higher elevations (Fei et al., 2018). Some
95 large lowland areas have also been converted to agricultural use, with rice and maize
96 being the most commonly cultivated crops (Belton & Fang, 2022; Sun et al., 2023;
97 You et al., 2014). Vast regions are also covered by Southeast Asian savannas,
98 characterized by tropical broadleaf evergreen trees (cover fraction smaller than 45%)
99 and usually C₄ grasses (Pletcher et al., 2022; Ratnam et al., 2016). In these
100 ecosystems, changes in precipitation patterns can largely affect the transpiration rates
101 and vegetation growth (Guan et al., 2015; Stott, 1990). Additionally, the intensity and
102 duration of the summer monsoon vary in response to the Indian and Pacific Ocean
103 dynamics, which can drastically reduce water availability for extended periods (Cook
104 et al., 2010; Nguyen et al., 2020). Therefore, understanding how vegetation responds
105 to climate drivers – such as temperature, relative humidity, precipitation, and solar
106 radiation – is crucial for enhancing our understanding of the ecohydrology of SEA
107 ecosystems and improving predictions of water availability and carbon fluxes in a
108 changing climate.

109 There are significantly fewer ecohydrology studies in SEA compared to other tropical
110 regions (e.g., Amazon), and little is known about how plants respond to environmental
111 variables and how this response varies across water availability and latitudinal
112 gradients (Huete et al., 2008; Qian et al., 2019; Satriawan et al., 2024; Zhao et al.,
113 2024). Most of the previous studies focused on a specific area or region, making it
114 difficult to generalize the results across larger scales or over the entire SEA (Alberto
115 et al., 2011; Fei et al., 2018; Li et al., 2010; Vu et al., 2023; Yang et al., 2023; Yuan
116 Zhang et al., 2016). For example, using flux tower data, Fei et al. (2018) found that
117 temperature is the main driver of carbon sinks in a tropical forest of SEA, while
118 precipitation is the primary driver in a savanna. Combining different remote sensing



119 datasets, Zhang et al. (2016) indicated that the GPP of tropical forests is mostly
120 affected by solar radiation during the wet season. Concurrently, Guan et al. (2015)
121 found that GPP of tropical forests decreases with water stress, when the total annual
122 precipitation falls below 2000 mm year⁻¹, suggesting that there are conditions where
123 water availability is still the limiting factor of plant photosynthesis. These findings
124 highlight the need for a deeper understanding and generalization of the mechanisms
125 controlling carbon and water cycle in SEA and the identification of the primary
126 climate drivers (e.g., air temperature, relative humidity, precipitation, solar radiation,
127 and wind speed) across the large latitudinal and vegetation cover gradients of SEA.

128 Leveraging on a compilation of existing flux tower data, and mostly on the
129 capabilities of a mechanistic ecohydrological model T&C (Fatichi et al., 2012a,
130 2012b), we conducted a series of numerical experiments (e.g., Fei et al., 2018;
131 Mastrotheodoros et al., 2019) to quantify water, energy, and carbon exchanges in 20
132 sites across the whole SEA. More specifically, this study addresses the following
133 questions: (i) What are the baseline magnitudes of current ET, GPP, and other
134 ecohydrological variables in terrestrial ecosystems across Southeast Asia? (ii) How do
135 ET, GPP, and other ecohydrological variables respond to perturbations in climate
136 drivers, such as air temperature, relative humidity, precipitation, solar radiation, and
137 wind speed? By addressing these questions, we contribute new knowledge to the
138 ecohydrological functioning of different ecosystems in an understudied region of the
139 Earth.

140 **2 Method**

141 To better understand the landcover types of SEA and to assess whether the available
142 flux tower sites represent the majority of these types, we first reconstructed the



landcover map of SEA based on available remote sensing products. We then set up a mechanistic ecohydrological model for existing flux tower sites and analysed the correlation between ecohydrological variables and climate drivers. Lastly, we conducted virtual experiments in terms of sensitivity analysis to understand the main drivers of ecohydrological variables in SEA.

2.1 Landcover maps of SEA

To better represent the landcover changes of SEA during recent years, we reconstructed a 1 km resolution landcover map for the year of 2022 by elaborating on available land cover maps derived from remote sensing datasets. This includes the databases of: MODIS landcover datasets (MCD12Q1), global forest watch, crop area and types, rubber plantation extent, oil palm plantation extent, and glacier cover area (Table 1). Specifically, we used the MODIS landcover map of year 2022 (Friedl et al., 2002; Friedl et al., 2010) as the base map, then overlaid the forest loss map from global forest watch (Hansen et al., 2013) to extract the cumulative areas that have changed over the last 20 years. Due to the forest watch map having much higher resolution (30m) than MODIS data (500m), we only assume that MODIS landcover pixel is changed when more than 60% of its area has lost forests. For these forest loss areas, we overlapped the crop-related datasets, rubber plantation, and oil palm data to update the MODIS basemap with their corresponding vegetation types.

Table 1. Datasets used for reconstructing a combined landcover map for Southeast Asia

| Data | Period | Resolution | Region | References |
|---------------------------|-----------|------------|----------------|--|
| MODIS landcover (MCD12Q1) | 2001-2022 | 500m | Global | (Friedl et al., 2002; Friedl et al., 2010) |
| Global forest watch | 2000-2022 | 30m | Global | (Hansen et al., 2013) |
| Rubber plantation | 1993-2016 | 10m | Southeast Asia | (Wang et al., 2023) |
| Oil Palm | 2019 | 10m | Global | (Descals et al., 2021) |



| | | | | |
|------------------------|-----------|---------|------------------------|------------------------|
| Oil Palm | 2001-2016 | 100m | Malaysia and Indonesia | (Xu et al., 2020) |
| Crop area | 2003-2019 | 30m | Global | (Potapov et al., 2022) |
| Crop types (SPAM 2010) | 2010 | 10km | Global | (You et al., 2014) |
| Glacier data (GAMDAM) | 2018 | Polygon | Asia | (Sakai, 2019) |

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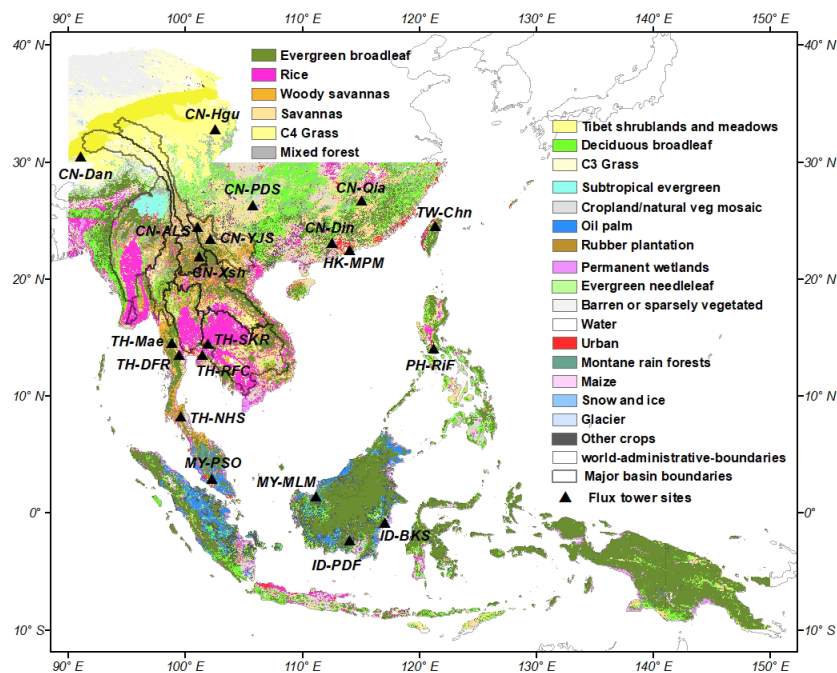
165 2.2 Flux tower sites

166 We utilized available data from 20 flux tower sites located across SEA for our
167 analysis and numerical experiments. These flux tower sites span a wide range of
168 latitudes and climate gradients, extending from the Tibetan Plateau to Equatorial
169 regions (Figure 1). The mean annual precipitation across these sites varies from 520 to
170 4762 mm year⁻¹, whereas the mean annual air temperature ranges from 1.8 °C to
171 28 °C (Table 2). The vegetation types include evergreen broadleaf forests (which
172 covers 33.8% of SEA), savannas and woody savannas (15.5%), deciduous broadleaf
173 forest (12.7%), rice field (10.2%), mixed forest (4%), C₃ grasslands (3.6%), mangrove
174 and wetlands (2%), C₄ grasslands (1.4%), evergreen needleleaf forests (1.2%), rubber
175 plantation (0.6%) and montane cloud forests (0.2%). Therefore, the analysed sites
176 cover all of the main vegetation types of SEA, except for oil palm and maize, which
177 account for 3% and 3.5% of land cover in SEA, respectively. Detailed information on
178 the 20 flux tower sites and associated references is provided in Table 2.

179 Due to the large uncertainties in energy flux measurements (e.g., leading to energy
180 closure problems, as in Table 2) with most observations collected in complex
181 environmental conditions, the lower quality standardization protocols for raw data
182 processing for some of the sites, as compared to standards assumed in Fluxnet-2015
183 (Pastorello et al., 2020), and the numerous data gaps, we treat the observed fluxes



184 only as an indication of model performance. Instead, we rely on simulations of a well-
185 tested ecohydrological model to compute all the long-term means and statistics.



186
187 *Figure 1. The reconstructed landcover map of Southeast Asia for year 2022 and*
188 *locations of flux tower sites used for studying the carbon and water cycles in this*
189 *region. We include the southern part of the Tibetan region because it is the source*
190 *area of the Mekong and Salween rivers.*

191
192 *Table 2. Characteristics of flux tower sites. These characteristics include the main*
193 *biome, latitude, longitude, elevation, measurement available period, mean annual*
194 *precipitation (P_r), mean air temperature (T_a), mean short wave radiation (R_{sw}), mean*
195 *vapor pressure deficit (VPD), mean relative humidity (R_h), and energy balance*
196 *closure (EC) calculated as the average of the sum of latent heat and sensible heat*
197 *fluxes normalized by net radiation at daily scale, and references of original studies for*
198 *these flux tower sites.*

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| Site | Name | Biome | Lat | Long | Elev (m a.s.l.) | Period | Mean Pr (mm year ⁻¹) | T _a (°C) | R _{sw} (W m ⁻²) | VPD (Pa) | R _a (%) | EC (%) | References |
|--------|-----------------------------------|-----------------------------------|--------|--------|--------------------|-----------|-------------------------------------|------------------------|---|-------------|-----------------------|-----------|---------------------------|
| ID-PDF | Palangkaraya drained forest | Tropical forest | -2.345 | 114.04 | 30 | 2002-2005 | 2331 | 26.3 | 198 | 791 | 78 | 85 | (Hirano et al., 2007) |
| ID-BKS | Bukit Soelarto | Tropical forest | -0.83 | 117.05 | 20 | 2001-2002 | 2276 | 26.5 | 169 | 567 | 84 | 40 | (GAMFO, 2005) |
| MY-MLM | Malidam | Tropical peat swamp forest | 1.45 | 111.15 | 3 | 2014-2015 | 2902 | 27.1 | 202 | 351 | 90 | NA | (Busman et al., 2023) |
| MY-PSO | Pasoh Forest Reserve | Tropical forest | 2.966 | 102.3 | 100 | 2003-2009 | 1865 | 25.3 | 198 | 629 | 81 | 99 | (Takamashi et al., 2010) |
| TH-NHS | Nakhon Si Thammarat | Rubber plantation | 8.32 | 99.58 | 200 | 2017-2018 | 2827 | 26.4 | 186 | 565 | 84 | 103 | (Ujjan et al., 2017) |
| TH-RFC | Rubber Flux Chachoengsao | Rubber plantation | 13.57 | 101.46 | 69 | 2015-2018 | 1467 | 27.6 | 205 | 785 | 79 | 97 | (Kampanon et al., 2015) |
| TH-DFR | Dry Dipterocarp Forest Ratchaburi | Tropical dry deciduous | 13.58 | 99.50 | 118 | 2015-2017 | 1405 | 27.2 | 212 | 1005 | 72 | 100 | (Sanwangsri et al., 2017) |
| PH-RIF | Philippine Rice Institute Flooded | Crop rice | 14.14 | 121.26 | 27 | 2012-2014 | 2729 | 26.5 | 180 | 880 | 75 | 81 | (Alberto et al., 2014) |
| TH-SKR | Sakarat | Tropical dry deciduous | 14.49 | 101.91 | 543 | 2001-2003 | 1483 | 24.2 | 198 | 943 | 69 | 87 | (Ichii et al., 2017) |
| TH-Mae | Mae Klong | Tropical dry deciduous | 14.57 | 98.84 | 231 | 2003-2004 | 1361 | 24.8 | 202 | 1004 | 69 | NA | (Ichii et al., 2017) |
| CN-Xsh | Xishuangbanna | Subtropical evergreen broadleaf | 21.95 | 101.20 | 756 | 2003-2005 | 1312 | 21.2 | 149 | 614 | 76 | 52 | (Zhang et al., 2006) |
| HK-MPM | Mai Po Mangrove | Mangrove | 22.49 | 114.03 | 0 | 2016-2018 | 1843 | 23.7 | 164 | 645 | 77 | 97 | (Lin & Lai, 2019) |
| CN-Din | Dinghushan | Subtropical evergreen broadleaf | 23.17 | 112.53 | 300 | 2003-2005 | 1374 | 20.4 | 139 | 669 | 71 | 47 | (Wang et al., 2006) |
| CN-YJS | Yuanjiang | Savanna with C ₄ grass | 23.47 | 102.17 | 553 | 2013-2015 | 630 | 24.2 | 195 | 1370 | 57 | 52 | (Fei et al., 2017) |
| CN-ALS | AilaoShan | Mixed forest | 24.54 | 101.03 | 2500 | 2009-2013 | 1890 | 11.6 | 158 | 326 | 74 | 100 | (Song et al., 2017) |
| TW-Cin | Chil'an mountain | Montane cloud forest | 24.58 | 121.4 | 1650 | 2007-2009 | 4763 | 14.5 | 116 | 138 | 91 | 120 | (Hsieh et al., 2008) |
| CN-PDS | Puding | Savanna with C ₄ grass | 26.35 | 105.75 | 1170 | 2015-2019 | 1327 | 16.3 | 133 | 429 | 79 | 47 | (Wang et al., 2020) |
| CN-Qia | Qianranzhou | Evergreen needleleaf | 26.14 | 115.06 | 109 | 2003-2005 | 1170 | 18.2 | 141 | 702 | 72 | 78 | (Yu et al., 2006) |
| CN-Dan | Dangxiong | Grassland C ₃ | 30.49 | 91.06 | 4330 | 2004-2005 | 520 | 2.2 | 221 | 404 | 42 | 126 | (Shi et al., 2006) |
| CN-Hgu | Hongyuan | Grassland C ₃ | 32.84 | 102.59 | 3500 | 2015-2017 | 778 | 3.0 | 206 | 325 | 62 | 110 | (Peng et al., 2011) |



204 2.2 Mechanistic ecohydrological model

205 We utilized the mechanistic ecohydrological (terrestrial biosphere) model T&C,
206 which resolves the coupled dynamics of water, energy, and carbon fluxes at the land
207 surface at the hourly scale (e.g., Fatichi et al., 2012a, 2012b; Mastrotheodoros et al.,
208 2019; Meili et al., 2024; Paschalis et al., 2024). Specifically, T&C simulates the
209 hydrological processes including canopy interception and evaporation, transpiration,
210 ground evaporation, infiltration, surface runoff and subsurface lateral and vertical
211 flow (Mastrotheodoros et al., 2020). In addition, it simulates dynamic vegetation
212 processes, including photosynthesis, carbon allocation to different plant compartments
213 (e.g., leaves, sapwood, hardwood, fine roots), respiration, and tissue turnover, at daily
214 scales. T&C also simulates phenology based on a multi-criteria scheme which
215 considers the effect of temperature, soil moisture, incoming radiation, and length of
216 the photoperiod (Fatichi et al., 2012a).

217 We used the observational data from 20 flux towers to compare with T&C simulations
218 across these sites and identify suitable parameters. We then used hourly
219 meteorological forcing observed at the flux towers (ranging from 1 to 7 years) as a
220 baseline climate inputs for the numerical experiments. The T&C model has been
221 widely applied and tested across various climate and ecosystems (Fatichi et al., 2014;
222 Z. Luo et al., 2024; Manoli et al., 2018; Meili et al., 2024; Moustakis et al., 2022;
223 Pappas et al., 2016) and it is further tested here. A detailed description of T&C model
224 can be found in the aforementioned publications.

225 2.3 Numerical simulations and perturbation experiments

226 We began by performing a correlation analysis to examine the relationship between
227 ecohydrological variables (at annual scales) including ET, GPP, water use efficiency



(WUE, calculated as $GPP/Transpiration$), carbon use efficiency (CUE, calculated as GPP/NPP with NPP being the net primary productivity) and key climate drivers (i.e., annual mean air temperature T_a , relative humidity R_h , short wave radiation R_{sw} , net radiation R_n , precipitation P_r , and wind speed W_s). Following this analysis of the simulations for the current climate, we conducted numerical experiments to investigate how ecohydrological variables respond to the changes in climate drivers such as air temperature, relative humidity, precipitation, solar radiation, and wind speed. As all these variables have different temporal variability and units – in order to make the responses of ecohydrological fluxes comparable across different climate drivers perturbations for a given location and across locations – we adjusted the climate inputs by increasing or decreasing them by one and two standard deviations (SD) of the magnitude of interannual variability (Mastrotheodoros et al., 2019). Given that most flux towers have data of less than five years (Table 2), we used ERA5 hourly data over 1981-2022 (Hersbach et al., 2020) to obtain the annual means of meteorological variables to calculate the annual SD over the 41 years of ERA5 product for each variable. The SD of each climate variable is a single value for the entire record. From the ERA5 dataset, we extracted air temperature at 2-meter height, wind speed components at 10 meters, dew point temperature at 2 meters, and mean surface downward shortwave radiation. ERA5 precipitation has limitations and is deemed less reliable in tropical regions (Lavers et al., 2022). Therefore, we used precipitation data obtained from the Climate Hazards Group Infrared Precipitation with Stations (CHIRPS, Funk et al., 2015).

In the perturbation experiment, we modified the time series of each climate variables by applying four scenarios that shifted the mean of the resulting time series by one or two SDs relative to the original. Specifically, we perturbed each climate variable by



253 adding/subtracting or multiplying by a scaling factor using: (i) plus one and (ii) two
254 SDs and (iii) minus one and (iv) two SDs of the original climate variables. Daily
255 cycles and seasonal variability are thus just shifted by these perturbation values. For
256 perturbation of solar radiation, we adjust the direct and diffuse radiation
257 proportionally, applying the same SDs change to both. As most of the flux tower sites
258 have observations for only two or three years (Table 2), which may cause the results
259 to be strongly influenced by the initialization of vegetation carbon pools, we ran the
260 perturbation and the baseline experiments for all 20 sites for the same length of six
261 years, which is twice of the average length of all flux tower sites, by repeating the
262 available meteorological inputs in a concatenated sequence. Then we calculate the
263 difference between the perturbed scenarios and the baseline to analyse the sensitivity
264 of ecohydrological variables to climate drivers.

265 Air temperature changes affect relative humidity and vapor pressure deficit (VPD). To
266 disentangle their individual effects, we tested three different methods of perturbing air
267 temperature: (i) we change the air temperature, but do not change the relative
268 humidity; (ii) we change the air temperature, but we do not change the vapor pressure,
269 so the relative humidity is modified; (iii) we change the air temperature, but we do not
270 change the VPD, so both relative humidity and vapor pressure are different. Out of
271 the three different methods, method (iii) can represent the most direct air temperature
272 effect because it keeps VPD the same. The other two methods represent a combined
273 effect of perturbed air temperature and VPD, because VPD changes with air
274 temperature. It changes more in the method (ii) as vapor pressure is not allowed to
275 increase. More detailed equations for the three perturbation methods can be found in
276 supplementary material section S1.

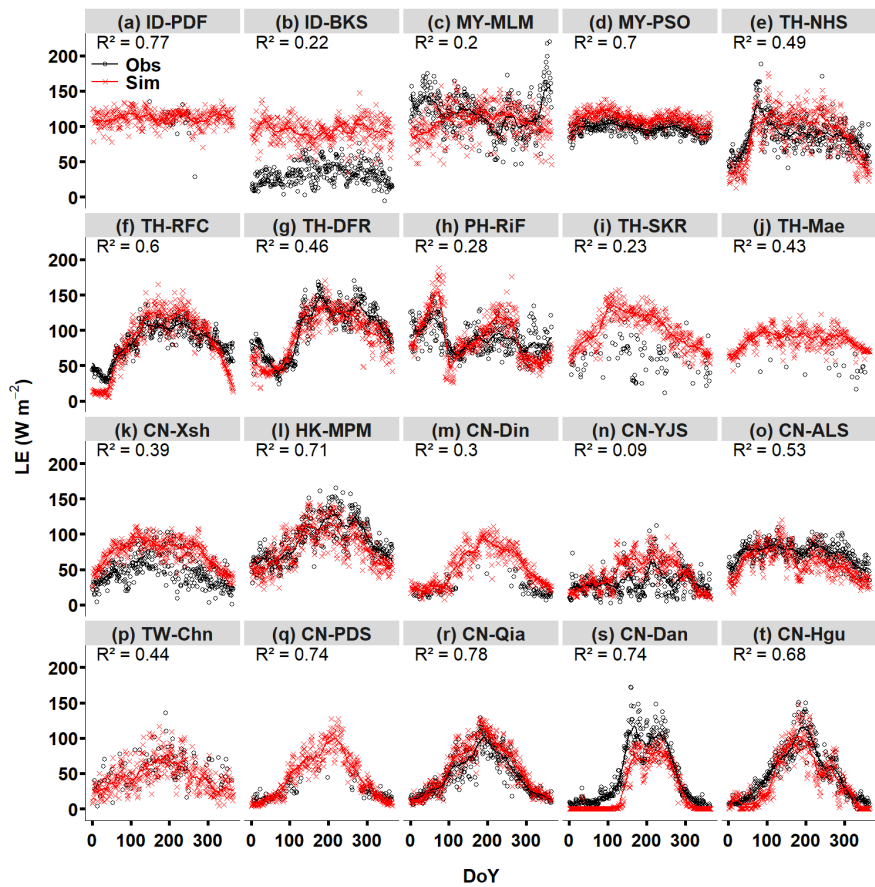


277 **3 Results**

278 3.1 Model validation

279 The energy and carbon fluxes, including net radiation (R_n), sensible heat (H), latent
280 heat (LE), and GPP, are used to validate the T&C model. Considering the very large
281 uncertainty in the data, the model performance is generally good in capturing these
282 fluxes across 20 sites (Table 3, Figure 2, Figure S1, S2 and S3) with few exceptions.
283 The seasonality of simulated energy fluxes is generally well matched with
284 observations except for certain nonseasonal sites such as ID-BKS and MY-MLM
285 (Figure 2). There are also many stations that do not report GPP as the Net Ecosystem
286 Exchange observations were not processed; however, for sites where data are
287 available, the model can capture the seasonality and magnitude of GPP generally well,
288 except for MY-MLM and CH-YJS (Figure S3, Table 3). Given the short duration and
289 the limited quality of flux-tower observations in certain challenging ecosystems, see
290 for instance the large lack of energy balance closure (Table 2), we consider the overall
291 model skill satisfactory for the objective of the study.

292



293

294 *Figure 2. Comparison of T&C model simulation with latent heat (LE) data from flux*
295 *towers. The mean daily latent heat is calculated for every day of year (DoY)*
296 *considering all of the years with observations. We also applied a moving average*
297 *method with a window of 30 days to calculate the smoothed seasonality (the*
298 *continuous line) of observed and simulated LE. Coefficient of determination (R^2) of*
299 *simulated vs. observed LE at the daily scale are shown at the top left for each site.*

300

301 *Table 3. Coefficient of determination (R^2) between the simulated and observed daily*
302 *energy and carbon fluxes for 20 flux sites. NA indicates no data available from flux*
303 *tower sites.*

| Flux sites | Net radiation | Latent heat | Sensible heat | GPP |
|------------|---------------|-------------|---------------|------|
| ID-PDF | 0.9 | 0.77 | 0.18 | NA |
| ID-BKS | 0.42 | 0.22 | 0.21 | NA |
| MY-MLM | NA | 0.2 | 0.17 | 0.22 |
| MY-PSO | 0.94 | 0.7 | 0.56 | NA |
| TH-NHS | 0.61 | 0.49 | 0.005 | 0.54 |



| | | | | |
|--------|------|------|------|------|
| TH-RFC | 0.55 | 0.6 | 0.46 | 0.59 |
| TH-DFR | 0.54 | 0.46 | 0.47 | 0.48 |
| PH-RiF | 0.52 | 0.28 | 0.53 | 0.67 |
| TH-SKR | 0.88 | 0.23 | 0.34 | NA |
| TH-Mae | 0.91 | 0.43 | NA | NA |
| CN-Xsh | 0.87 | 0.39 | 0.1 | NA |
| HK-MPM | 0.95 | 0.71 | 0.58 | 0.54 |
| CN-Din | 0.08 | 0.3 | 0.01 | 0.35 |
| CN-YJS | 0.83 | 0.09 | 0.19 | 0.14 |
| CN-ALS | 0.88 | 0.53 | 0.25 | 0.51 |
| TW-Chn | 0.92 | 0.44 | 0.69 | NA |
| CN-PDS | 0.97 | 0.74 | 0.46 | 0.78 |
| CN-Qia | 0.98 | 0.78 | 0.61 | 0.82 |
| CN-Dan | 0.91 | 0.74 | 0.49 | 0.66 |
| CN-Hgu | 0.65 | 0.68 | 0.1 | NA |

304

305 3.2 Correlation analysis

306 We analyse the correlation between simulated ET and GPP (Table 4, Figure 3) and
307 various climate drivers across the 20 sites. At annual scale and across sites, ET
308 exhibits the strongest correlation with net radiation (Figure 3d, $R^2 = 0.73$), while it
309 shows relatively weaker correlations with precipitation ($R^2 = 0.2$) and wind speed (R^2
310 $= 0.16$). ET increases with air temperature ($R^2 = 0.55$) in general, though the
311 correlation is weaker as compared with simulated net radiation (Figure 3a). As net
312 radiation is a model output, ET is directly conditioned upon it and there is circularity
313 in its effects on ET. As a result, the air temperature has the strongest correlation with
314 ET among the independent input variables. This remarks how SEA is primarily an
315 energy-limited region and precipitation has only an influence on high latitudes sites in
316 the Tibetan plateau, which tend to be both temperature and water-limited, contrary to
317 most of the other sites below 20° latitude (Figure 3e), which do not show evidence of
318 water limitations at the annual scale.

319 Unlike other climate drivers, across sites wind speed has a negative correlation with
320 ET because these high wind speed sites are predominantly located in high latitudes



and especially the Tibetan plateau, where ET is much lower (Figure 3f). The low ET values are not caused by high winds, but the covariation of wind with other climate variables leads to this negative correlation pattern. In summary, at the annual scale sites across SEA are largely energy-limited, with a few exceptions usually located at higher latitude.

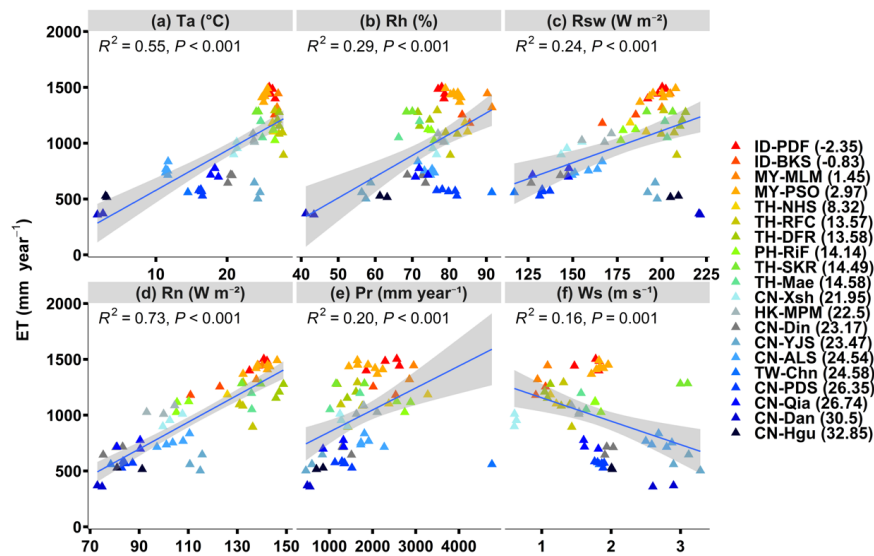


Figure 3. Correlation between annual climate drivers and simulated annual ET across sites. Data points are color-coded to represent flux tower sites at different latitudes. The grey band indicates the 95% confidence intervals of the linear regression line.

Table 4. Flux sites characteristics from T&C model simulations at mean annual scale include evapotranspiration (ET), net radiation (R_n), sensible heat (H), latent heat (LE), gross primary productivity (GPP), and Evaporative ratio (ET/ P_r).

| Flux Sites | ET (mm year ⁻¹) | Rn (W m ⁻²) | H (W m ⁻²) | LE (W m ⁻²) | GPP (gC m ⁻² year ⁻¹) | Evaporative ratio |
|------------|--------------------------------|----------------------------|---------------------------|----------------------------|---|----------------------|
| ID-PDF | 1457 | 139 | 23 | 112 | 3190 | 0.63 |
| ID-BKS | 1217 | 117 | 20 | 94 | 2861 | 0.53 |
| MY-MLM | 1382 | 139 | 28 | 107 | 3475 | 0.48 |
| MY-PSO | 1432 | 140 | 26 | 110 | 3247 | 0.77 |



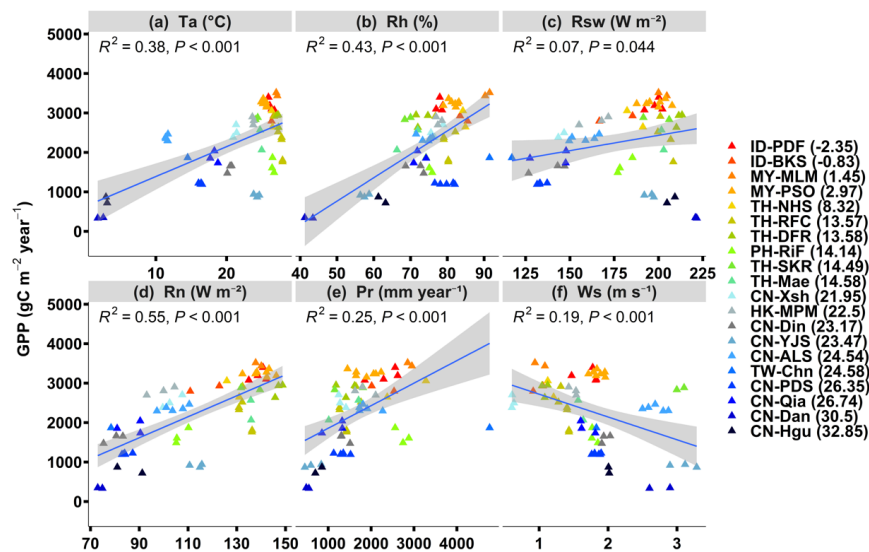
| | | | | | | |
|--------|------|-----|----|----|------|------|
| TH-NHS | 1143 | 128 | 38 | 88 | 2852 | 0.40 |
| TH-RFC | 1059 | 133 | 50 | 81 | 2284 | 0.72 |
| TH-DFR | 1213 | 147 | 51 | 93 | 2840 | 0.86 |
| PH-RiF | 1088 | 107 | 14 | 91 | 1655 | 0.40 |
| TH-SKR | 1282 | 136 | 34 | 99 | 2859 | 0.86 |
| TH-Mae | 1124 | 136 | 47 | 87 | 2315 | 0.83 |
| CN-Xsh | 954 | 103 | 26 | 74 | 2527 | 0.73 |
| HK-MPM | 1041 | 99 | 14 | 82 | 2801 | 0.56 |
| CN-Din | 691 | 80 | 24 | 53 | 1596 | 0.50 |
| CN-YJS | 569 | 114 | 69 | 44 | 908 | 0.90 |
| CN-ALS | 761 | 104 | 42 | 60 | 2359 | 0.40 |
| TW-Chn | 559 | 78 | 33 | 43 | 1867 | 0.12 |
| CN-PDS | 566 | 84 | 40 | 44 | 1205 | 0.43 |
| CN-Qia | 730 | 87 | 29 | 56 | 1876 | 0.62 |
| CN-Dan | 364 | 74 | 49 | 29 | 341 | 0.70 |
| CN-Hgu | 522 | 86 | 44 | 41 | 795 | 0.67 |

333

334 GPP across sites remains strongly correlated with net radiation ($R^2 = 0.55$), but the
335 correlation coefficients are smaller as compared to ET (Figure 4d). In contrast to ET,
336 GPP is not strongly related to shortwave radiation; this is mostly due to a few sites in
337 the Tibetan plateau that have very low GPP (temperature and water-limited), despite
338 receiving high loads of shortwave radiation (Figure 4c). These sites are, however,
339 characterized by proportionally higher sensible heat and lower net radiation (Table 4).
340 At latitudes lower than 24° the correlation between GPP and shortwave radiation is
341 stronger ($R^2 = 0.13$). Moreover, GPP has a stronger correlation ($R^2 = 0.44$) with



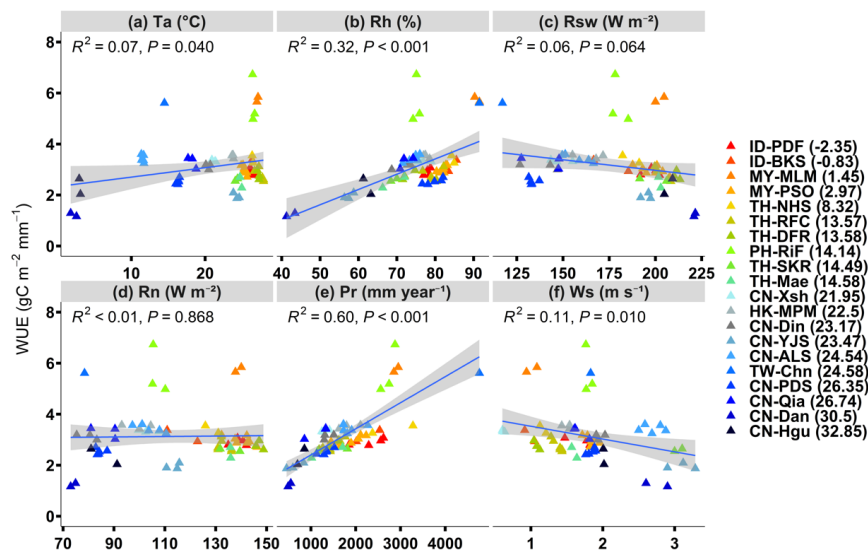
342 relative humidity than ET (Figure 4b). Lower relative humidity leads to higher VPD
343 which induces stomatal closure (Sabot et al., 2022) and thus less photosynthesis given
344 other conditions are the same; this affects GPP more than ET as the latter is still
345 mainly driven by the higher VPD compensating for the stomatal closure. Higher
346 relative humidity sites have also more cloud cover and diffuse light to plants which
347 enhances light use efficiency (Figure S4, Xu et al., 2023). GPP also showed a
348 relatively weak correlation with air temperature, especially for tropical and
349 subtropical sites where higher temperatures do not lead to more GPP (Figure 4a). This
350 suggests that for these tropical and subtropical sites, the temperature for growth has
351 reached its optimum in the model simulations and GPP is limited by other factors,
352 such as radiation and humidity. In summary, GPP in SEA exhibits less climate driven
353 relationships compared to ET, which are largely mediated by humidity and radiation
354 at lower latitudes with temperature and precipitation playing a more pronounced role
355 for a few sites as CN-YJS, CN-Dan, and CN-Hgu.



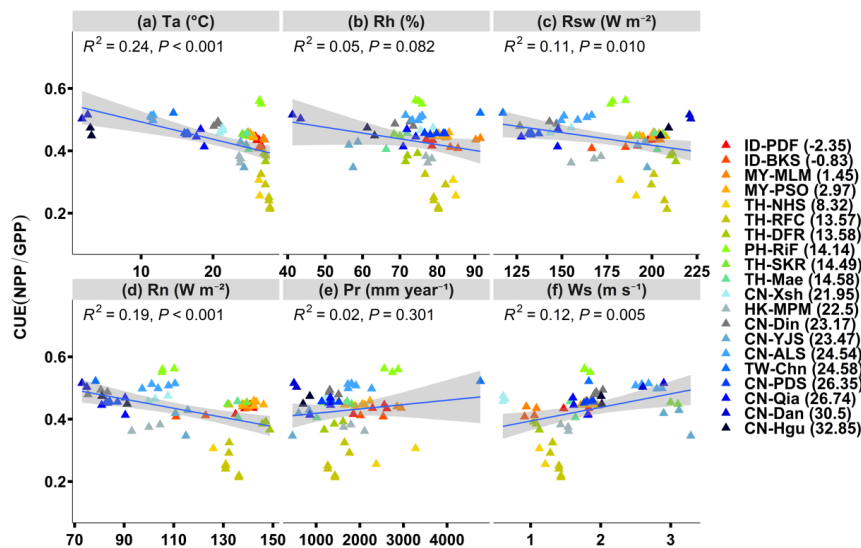
356

357 *Figure 4. Correlation between annual climate drivers and simulated annual GPP*
358 *across sites. Data points are color-coded to represent flux tower sites at different*
359 *latitudes. The grey band indicates the 95% confidence intervals of the linear*
360 *regression line.*

361 WUE is strongly correlated with precipitation, with higher precipitation leading to
362 larger WUE (Figure 5e). Moreover, it does not exhibit correlation with net radiation,
363 which is very different from the behaviours of ET and GPP (Figure 5d). WUE also
364 shows a very weak and not statistically significant correlation with air temperature
365 and shortwave radiation. The correlation analysis suggests that plants in wetter
366 regions have a higher WUE (at annual scales) than those in drier regions, following
367 global patterns (Fatichi et al., 2023). Additionally, the rice field (PH-RiF) and swamp
368 forest (MY-MLM) exhibit a much higher WUE (Figure 5e), which is due to the very
369 high relative humidity suppressing the transpiration during the growing season (Table
370 2).



371
372 *Figure 5. Correlation between annual climate drivers and simulated annual WUE*
373 *across sites. WUE is calculated as the ratio between annual GPP and transpiration.*
374 *Data points are color-coded to represent flux tower sites at different latitudes. The*
375 *grey band indicates the 95% confidence intervals of the linear regression line.*
376 CUE shows a relatively weak correlation with all climate variables with air
377 temperature having the highest correlation ($R^2 = 0.24$) and no correlation with
378 precipitation and relative humidity ($p\text{-value} > 0.05$, Figure 6). CUE generally decreases
379 with higher temperatures, as higher temperature exerts a higher toll on plant
380 maintenance respiration leaving less carbon for growth. Moreover, CUE also
381 decreases with increasing shortwave radiation, although the correlation is relatively
382 weak. These findings are consistent with recent global studies that CUE generally
383 decreases with higher light availability and temperature (Luo et al., 2025). However,
384 the weak correlations between CUE and climate drivers indicates that carbon use
385 efficiency tends to be quite stable across climates and ecosystems (De Lucia et al.,
386 2007).



387
388 *Figure 6. Correlation between annual climate drivers and simulated annual CUE*
389 *across sites. Data points are color-coded to represent flux tower sites at different*
390 *latitudes. The grey band indicates the 95% confidence intervals of the linear*
391 *regression line.*
392 3.3 Sensitivity of ET to climatic variables in the perturbation experiments
393 The pure effect of modifying air temperature (from method iii) has a small influence
394 in changes in ET, with most of the responses being within $\pm 50 \text{ mm year}^{-1}$, ($\pm 5\%$),
395 while modifying relative humidity has the strongest effects, with most of the
396 responses spanning within a range of $\pm 125 \text{ mm year}^{-1}$ ($\pm 12\%$) with a largely linear
397 response (Figure 7). Regarding relative humidity changes, the most responsive sites
398 are the CN-ALS mixed forest (2.1% decrease of ET for 1% increase in R_h) and TW-
399 Chn montane cloud forest (2.7% decrease of ET for 1% increase in R_h , Table S1),
400 both located in high-elevation mountain regions with very low VPD baseline and
401 sufficient precipitation (Figure 7I, Table 2). In contrast, the least sensitive site is CN-
402 YJS, with almost no responses ($\sim 0.2\%$ decrease of ET for increase 1% in R_h) to
403 relative humidity changes, which is characterized by dry and water-limited conditions



404 (Figure 7G, Table S1). Although CN-YJS (valley) and CN-ALS (mountain) are
405 located at similar latitudes and relatively close to each other, elevation and associated
406 differences in water availability play a fundamental role in shaping their different
407 responses to climate.

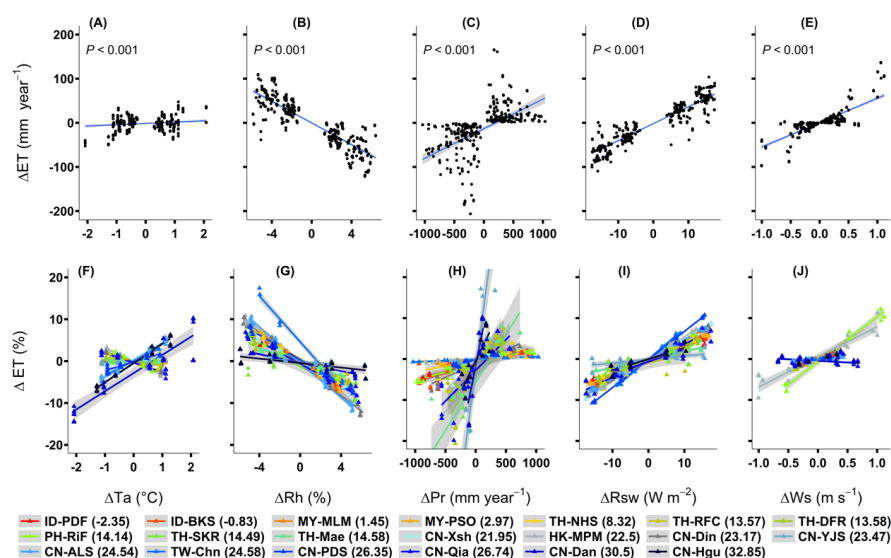
408 The different ways of perturbing specific humidity associated with a change in air
409 temperature have distinct effects on the ET responses (Figure S5), with method (ii)
410 having the strongest effect (with a range around $\pm 150 \text{ mm year}^{-1}$) as it generates the
411 largest VPD change, which reflects on ET. However, as highlighted by the different
412 perturbation methods, this is mostly a VPD effect rather than a pure air temperature
413 change. Modifying purely air temperature causes many tropical and subtropical sites
414 to even have a decrease of ET with higher air temperatures (Figure S5). This
415 decreasing trend is because plants operate beyond the optimal temperature for
416 photosynthesis and with higher temperatures there is a decrease of GPP and
417 consequently LAI, which leads to smaller ET (Huang et al., 2019).

418 Shortwave radiation also has a relatively significant effect because most of the
419 responses span a range of $\pm 100 \text{ mm year}^{-1}$ ($\pm 10\%$), and almost all sites show
420 increased ET with a higher shortwave radiation (Figure 7D). The TW-Chn cloud
421 montane forest, which is very limited by light availability, shows the largest
422 responsiveness to changes in solar radiation ($\sim 0.8\%$ for 1 W m^{-2}), while the Savanna
423 with C_4 grasses (CN-YJS) is the least affected (0.09% for 1 W m^{-2} , Figure 7I and
424 Table S1), as it is largely water-limited. This confirms that the TW-Chn has the
425 strongest energy limitations because of its persistent cloud cover and extremely high
426 relative humidity with an annual average $R_h = 91\%$, larger than tropical forests.
427 Regarding wind speed, most sites exhibit minimal responses (with a range of smaller
428 than 3% and 50 mm year^{-1} Figure 7E, J), except for the PH-RiF and HK-MPM sites



429 (larger than 7% for 1 m s⁻¹ changes in W_s). Both sites, a flooded rice field and a
430 mangrove, have ponding water at the surface for large period of times, a higher wind
431 speed reduces aerodynamic resistance below the canopy, which can enhance ET
432 especially from the ponding water surface.

433 ET sensitivity to precipitation varies significantly across different sites (Figure 7H).
434 Most sites located south of 14° N latitude show minimal response (smaller than 1%
435 for 100 mm year⁻¹ change in P_r) to changes in precipitation (Figure 7H, Table S1). In
436 contrast, sites on the Tibetan Plateau such as the C₃ grasslands (CN-Dan and CN-Hgu)
437 and the Savanna (CN-YJS) are very sensitive to precipitation changes (larger than 3%
438 for 100 mm year⁻¹ changes in P_r), showing that water limitations are shaping the
439 functioning of the ecosystem. Overall, the sensitivity analysis supports the finding
440 that SEA at large is much more energy-limited than water-limited with changes in
441 shortwave radiation and mostly relative humidity affecting ET at almost all of the
442 sites, with precipitation being important only at specific sites.



443

444 *Figure 7. ET responses to perturbation of various climate drivers, including air*
445 *temperature, relative humidity, precipitation, shortwave radiation, and wind speed.*
446 *The top panels show the absolute changes of ET, and the bottom panels show the*
447 *relative changes of ET in percentage. The air temperature perturbation with method*
448 *(iii) is reported to isolate the pure air temperature effect. Note that some of the*
449 *extreme points beyond the plotting range are not shown for visual clarity; however, all*
450 *data points were included in the regression fit.*

451 3.4 Sensitivity of GPP to climatic variables in the perturbation experiments

452 The responses of GPP to perturbations of climate drivers are more complex and less
453 consistent across different sites compared to ET (Figure 8). For the air temperature
454 effect, almost all the tropical and subtropical sites (south of 22.5°N) show a decrease
455 in GPP with warmer air temperatures (Figure 8F, Table S2). In the simulations,
456 additional warming at these high temperatures is moving vegetation away from
457 thermal optimum which is generally close to $28\text{--}29^{\circ}\text{C}$ for tropical regions (Huang et
458 al., 2019; Tan et al., 2017). Even though this effect is still debated in the literature
459 (Carter et al., 2024; Doughty et al., 2023; Smith et al., 2020), it seems plausible that
460 GPP decreases at temperatures higher than 28°C , even though thermal acclimation –
461 not accounted for in the T&C model – might mitigate this effect (Liu et al., 2024;



462 Oliver et al., 2025; Zarakas et al., 2024). For regions north of 22.5° N, GPP generally
463 increases with warmer temperature, which is due to the simulated extended growing
464 season of about 9 to 18 days, promoting GPP despite water limitations, as also
465 supported by empirical evidence (Grossiord et al., 2022). There is only one exception,
466 the CN-YJS savanna, where GPP declines with warmer temperature. This is due to an
467 enhancement of water stress, which is the dominant factor, since this site is warm and
468 dry (Table 2).

469 The pattern of GPP responses to air temperature changes is also consistent across
470 different methods of perturbing the air humidity associated with a temperature change
471 (Figure S6, Table S2). However, with method (ii), which produces the largest VPD
472 change, the magnitude of the GPP change is larger. In this case, the cooler
473 temperatures, which are tending toward the optimal range can lead to enhanced
474 photosynthesis and lower VPDs which further promote stomatal opening and
475 photosynthesis and lead to higher GPP (Figure S6 B and E, Doughty et al., 2023;
476 Igarashi et al., 2015; Zarakas et al., 2024). For example, the GPP of sites TH-DFR
477 decreases 123 gC m^{-2} (4.3%) for every 1° increase in air temperature with method
478 (iii), but decreases 206 gC m^{-2} (7%) in the method (ii) (Table S2). The differences of
479 GPP between method (ii) and method (iii) show that the temperature can have a
480 strong effect on photosynthesis regardless of VPD for tropical and subtropical
481 regions. On the other hand, GPP of a strongly thermally limited site as CN-Hgu
482 increases 135 gC m^{-2} (13%) for every 1° increase in air temperature in the method
483 (iii), but only increases 79 gC m^{-2} (7%) in the method (ii) as again higher VPD, which
484 causes stomatal closure and higher water stress counteracts the positive warming
485 effect on growing season length and photosynthesis rates.



486 GPP is most responsive to radiation changes with a range of $\pm 170 \text{ gC m}^{-2} \text{ year}^{-1}$ for
487 absolute changes and $\pm 7.5\%$ for relative changes (Figure 8 D and I). GPP generally
488 increases with higher solar radiation except for certain dry or cold regions such as
489 CN-YJS, CN-Dan, and CN-Hug (Figure 8I). More radiation enhances light
490 availability for photosynthesis and increase GPP. For instance, in tropical and sub-
491 tropical regions (south of 22.5°N) reducing shortwave radiation leads to lower GPP,
492 as less light is available for photosynthesis in these dense canopies. Colder regions in
493 the Tibetan plateau have sparse canopies and are already receiving quite a high solar
494 radiation load and the declines trend suggests that these sites do not benefit from
495 higher light availability (Figure 8I). The reduction in GPP at colder sites is an indirect
496 effect due to increased ET driven by higher energy available, which further decreases
497 soil moisture and lengthen the period when plants experience water stress. This occurs
498 also in the CN-YJS savanna, where GPP decreased in response to both higher air
499 temperature and solar radiation. This is the most water-limited ecosystem among
500 those analysed, with only 630 mm year^{-1} of precipitation and potential ET of 2587
501 mm year^{-1} and thus very vulnerable to drought conditions (Table 2).

502 The pattern of GPP responses to precipitation is similar to those of ET, with only the
503 drier sites (CN-Dan, CN-Hgu, CN-YJS) being sensitive with a $38 - 107 \text{ gC m}^{-2} \text{ year}^{-1}$
504 ($4.4 - 11.9\%$) increase in GPP for every 100 mm year^{-1} changes in precipitation (Table
505 S2), while most other sites have a change smaller than 2% , mostly controlled by leaf
506 wetness impacting photosynthesis (Figure 8H). The wind speed has a relatively small
507 effect; most of the sites have GPP changes smaller than 2% for every 1 m s^{-1} increase
508 in wind speed (Figure 8J, Table S2). Higher wind speed generally causes more GPP,
509 which is due to a lower aerodynamic resistance and leaf-boundary layer resistance
510 leading to higher CO_2 diffusion rate and enhanced photosynthesis rate (Damour et al.,



2010; Fatichi et al., 2023). Relative humidity also has a relatively small effect on GPP
(with a range of $\pm 40 \text{ gC m}^{-2}$ and $\pm 5\%$) but higher than wind speed (a range of $\pm 25 \text{ gC}$
 m^{-2} and $\pm 2.5\%$), with most sites increasing GPP with higher relative humidity,
particularly for the dry sites we mentioned earlier. This is due to higher relative
humidity (lower VPD) which leads to stomata opening and allows for higher CO_2
uptake and thus enhances GPP.

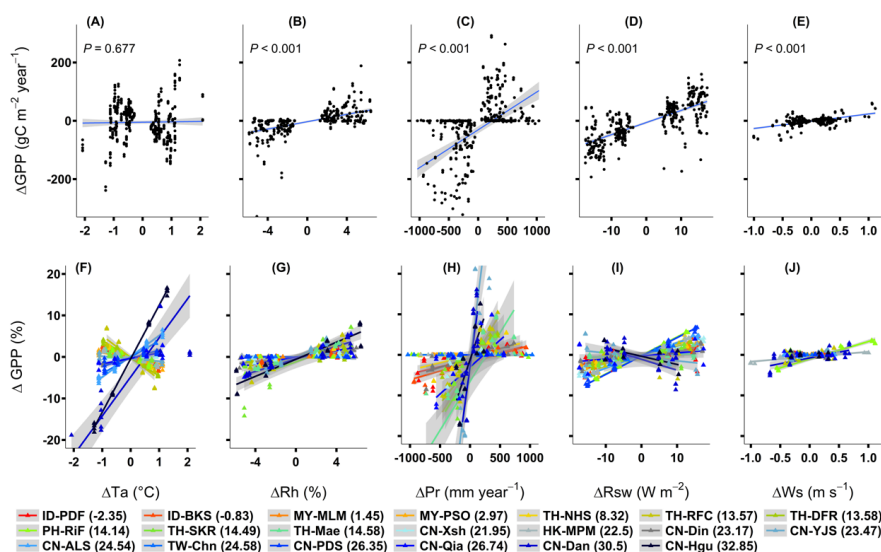


Figure 8. GPP responses to perturbation of various climate drivers, including air temperature, relative humidity, precipitation, short wave radiation, and wind speed. The top panels show the absolute changes of GPP, and the bottom panels show the relative changes of GPP in percentage. The air temperature perturbation with method (iii) is reported to isolate the pure air temperature effect. Note that some of the extreme points beyond the plotting range are not shown for visual clarity; however, all data points were included in the regression fit.

3.5 Sensitivity of WUE to climatic variables in the perturbation experiments

WUE is most sensitive to changes in relative humidity with a range of $\pm 0.5 \text{ gC m}^{-2} \text{ mm}^{-1}$ ($\pm 12\%$) and least sensitive to pure air temperature changes with a range of $\pm 0.125 \text{ gC m}^{-2} \text{ mm}^{-1}$ ($\pm 3\%$ for most points, Figure 9). In general, higher relative humidity leads to an increase in WUE across all sites, especially for already wet sites



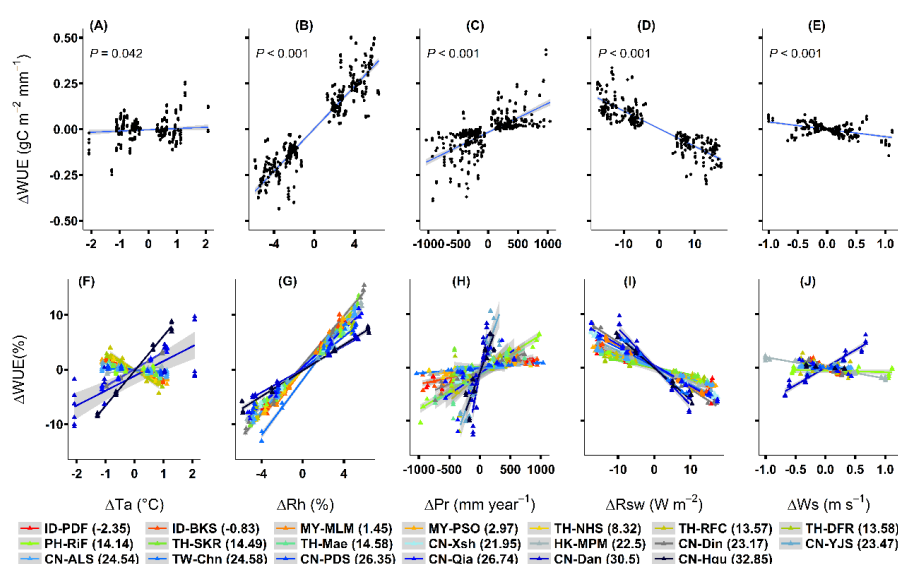
530 such as TW-Chn cloud forest and MY-MLM swamp forest. With higher relative
531 humidity, VPD decreases and causes a larger reduction of transpiration (larger than
532 1.5% per 1% changes in R_h) due to the reduced atmospheric demand but it does not
533 affect considerably stomatal aperture (e.g., Figure S5E and Figure S9E), while its
534 effect on GPP is negligible ($<0.01\%$ per 1% changes in R_h , Table S2) as GPP limited
535 by energy, leading to a considerably enhanced WUE.

536 Air temperature warming (pure, method iii) decreases WUE for most of the sites, with
537 reduced GPP and LAI being the dominant factor except at certain cold sites and sites
538 with standing water (Figure 9F). These sites show an increase in WUE with warmer
539 temperatures but for different reasons. For the colder sites such as CN-Dan and CN-
540 Hgu, warmer temperatures enhance GPP strongly ($\sim 10\%$ for 1°C changes in T_a , Table
541 S2) and affect transpiration only slightly ($\sim 4\%$, Table S1). For PH-RiF and HK-MPM,
542 where there is often ponding surface water, warmer temperatures can reduce
543 transpiration ($\sim 3.3\%$) slightly more than GPP ($\sim 2\%$, Table S2), which leads to higher
544 WUE. WUE responses to air temperature changes are different for different methods
545 of perturbing the associate humidity. For the method (ii), all sites show a decreasing
546 trend in WUE (larger than 9% per 1°C changes in T_a) with warming as VPD
547 increases. Results for method (i) shows very small responses (smaller than 4.5% for
548 most sites) to warming (Figure S7, Table S3).

549 Precipitation changes do not affect ($<1\%$ for increase 100 mm year^{-1} increase in P_r)
550 WUE in most tropical and subtropical sites as they are not modifying the water status
551 of plants (Figure 9H, Table S3). For the dry sites (i.e., CN-YJS, CN-Dan, CN-Hgu),
552 WUE increases substantially ($> 3.3\%$ for 100 mm year^{-1} increase in P_r) with more
553 precipitation, as this stimulates GPP and LAI with compounding effects on
554 productivity. Higher shortwave radiation decreases WUE for all sites, which is due to



555 it influencing more transpiration than GPP for humid sites and reducing GPP due to
556 enhanced water stress for dry sites. Higher wind speed generally decreases WUE,
557 which is due to transpiration increasing more than GPP in response to a smaller
558 aerodynamic resistance, except for the dry sites mentioned above. The increase in
559 WUE with higher wind speed in dry sites is due to the increased diffusion of CO₂,
560 which enhances GPP, while at the annual scale transpiration is unchanged as it is
561 largely dictated by precipitation.



562

563 *Figure 9. Water use efficiency (WUE, calculated as GPP/Trans) responses to*
564 *perturbations of climate drivers such as air temperature, relative humidity,*
565 *precipitation, shortwave radiation, and wind speed. The top panels are absolute*
566 *changes, and bottom panels are relative changes. The air temperature perturbation*
567 *with method (iii) is reported to isolate the pure air temperature effect. Note that some*
568 *of the extreme points beyond the plotting range are not shown for visual clarity;*
569 *however, all data points were included in the regression fit.*

570 3.6 Sensitivity of CUE to climatic variables in the perturbation experiments

571 CUE is most sensitive to air temperature changes, with warmer temperatures leading
572 to a lower CUE, which is due to enhanced maintenance respiration with warming
573 (Figure 10A and F). For every 1 °C increase in air temperature, there is more than



1.5% decrease in CUE. The most sensitive sites are the two rubber plantation sites (TH-NHS and TH-RFC) with a 4.7% - 7.4% drop of CUE for every 1 °C increase in air temperature, likely due to their higher allocation to non-structural carbohydrates, while the least responsive one is the CN-Dan in Tibetan plateau, with around 1% drop of CUE, as in there, temperature stimulates GPP as well. Moreover, these patterns are consistent across different perturbation methods of air temperature, which indicates that air temperature changes are the primary driver instead of the VPD changes (Figure S8). Generally, precipitation changes have a small effect (smaller than 0.7% for every 100 mm year⁻¹ changes) on CUE, except for the three dry sites (larger than 1.4%, CN-YJS, CN-Dan, CN-Hgu, Figure 10H, Table S4). For these three sites, higher productivity associated with more precipitation leads to higher LAI, a longer active season, and more respiration costs which, however, increase proportionally less than GPP.

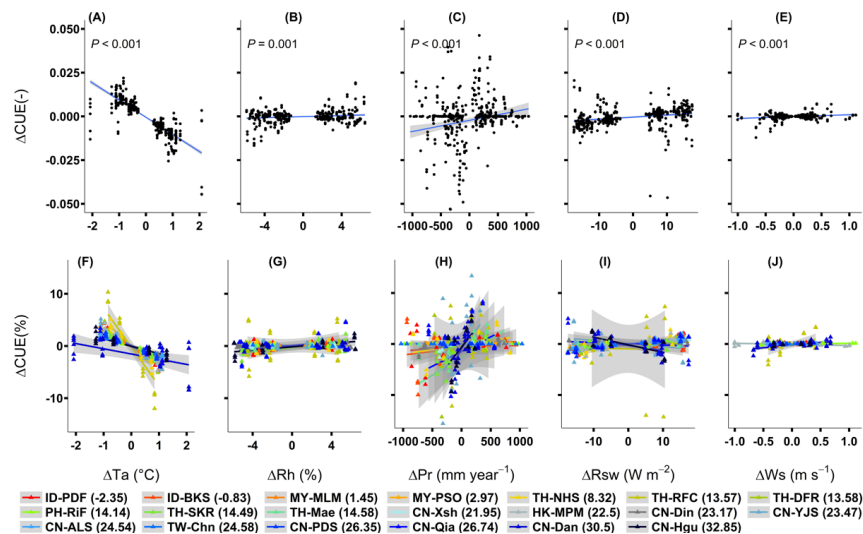


Figure 10. Same as Figure 9 but for carbon use efficiency (CUE), calculated as the ratio between NPP and GPP.



590 **4 Discussion**

591 4.1 An energy-limited region, with exceptions

592 The presented numerical experiments have shown that ET is most responsive to
593 relative humidity changes, while GPP showed the largest increase in response to
594 higher shortwave radiation (Figure 7B, Figure 8D). However, some dry sites, such as
595 the savanna and Tibetan Plateau grasslands, are water-limited ecosystems and respond
596 primarily to changes in precipitation (Figure 7H, Figure 8H). In summary, our virtual
597 experiments have remarked the degree to which SEA is an energy-limited region, but
598 they have also highlighted strong heterogeneities. For example, the CN-YJS Savanna,
599 despite being in the subtropical region, is highly a water-limited system as compared
600 to the other subtropical evergreen forests. Previous studies have highlighted that a
601 large area of SEA is covered by forest-savannas mosaics (more than 15.5%, Figure 1),
602 underscoring the importance of considering properly these understudied ecosystems
603 in the region (Ratnam et al 2016; Hamilton et al., 2024; Pletcher et al., 2022).
604 Elevation is another critical factor influencing ecosystem responses. For example,
605 TW-Chn and CN-ALS mountain receive much higher amount of precipitation than
606 sites located at similar latitudes and have higher relative humidity and lower solar
607 radiation (Table 2). Consequently, their ET is more energy-limited and exhibits
608 stronger responses to changes in relative humidity and radiation than other subtropical
609 forests (Figure 7, Table S1). Phenology also plays a critical role in determining
610 vegetation responses to climate drivers. Tropical dry deciduous forests (occupying
611 12.7% of the region) shed their leaves during the dry season as an adaptation strategy
612 to water stress conditions; this is different from subtropical evergreen forests (Reich,
613 1995; Vico et al., 2015; Zhang et al., 2016). Our study also found that the GPP of dry
614 deciduous forests (e.g., TH-SKR) has a response to precipitation changes stronger



615 than other subtropical evergreen forests, in turn suggesting that changes in
616 precipitation amount may affect these deciduous forests in a much more significant
617 way than other forests, at least for the precipitation perturbation analysed here
618 spanning 1-2 standard deviation of the interannual variability (Table S2, Figure 8H).

619 4.2 Limits of interpretation

620 There are several limitations and sources of uncertainty in our analysis. First, our
621 perturbation experiments did not account for the interactions between different
622 climate drivers, as we perturbed each driver individually. For example, when
623 perturbing the shortwave radiation we did not consider any land-atmospheric
624 feedbacks which may also affect temperature, precipitation, relative humidity and
625 wind speed (Laguë et al., 2019; Wang et al., 2025) The virtual experiments show the
626 opposite effect of increasing shortwave radiation and air temperature on ET and GPP
627 for tropical and subtropical regions (Table S1, Table S2). If the combined effect is
628 considered, the ET and GPP may not respond strongly to radiation changes. Secondly,
629 any of the virtual experiments did not consider the CO₂ fertilization effect that can
630 increase GPP and eventually LAI (Fatichi & Leuzinger, 2013; Yang et al., 2016).
631 Furthermore, we show that warmer temperatures and lower relative humidity both
632 decreased GPP for tropical and subtropical regions. However, higher CO₂
633 concentrations can buffer this trend with the potential for GPP to not decrease but
634 rather increase in a changing climate. Finally, while representative of many different
635 ecosystems and of the most prominent ecosystems – we analysed only 20 sites, due to
636 availability of meteorological forcing and flux tower data to constrain the model
637 simulations. The public release of existing carbon, water, and energy fluxes dataset in
638 the region (e.g., Kuricheva et al., 2021; Ueyama et al., 2025) or the installation of new
639 flux towers could be fundamental to extend such an analysis in the future.



640 4.3 Role of humidity and temperature

641 The virtual experiments have shown that relative humidity (or VPD) perturbations,
642 not the temperature perturbations, are the main driver of ET changes (Figure 7 A&B,
643 Table S1), while temperature changes generally have larger effect than VPD on GPP
644 for tropical and subtropical forests (Figure S6, Table S2). This study shed light on
645 how important is to disentangle the relative role of temperature and VPD on different
646 ecosystems. Temperature and humidity manipulation experiments could shed more
647 light on this aspect, but in the real world, it is challenging to separate temperature and
648 VPD effects in observations because they co-occur. However, it is important to
649 mechanistically understand how ecohydrological fluxes will respond to these two
650 drivers (Zarakas et al., 2024). Recent studies have found that the future cross-
651 correlation of temperature and VPD is non-stationary and can deviate from current
652 relationships because the land ET and moisture transport from ocean to land will not
653 be able to keep pace with the temperature increase over land under global warming
654 (Byrne, 2021; Byrne & O’Gorman, 2016, 2018). Observation studies have found that
655 VPD effects on photosynthesis are stronger than temperature effects in general (Fu et
656 al., 2018; Santos et al., 2018; Slot et al., 2024), but temperature effects are still
657 dominant for GPP in tropical regions (Doughty et al., 2023; Slot & Winter, 2017b,
658 2017a). The mechanistic ecohydrological simulations presented here corroborate these
659 findings.

660 **5 Conclusions**

661 Through a synthesis of data and mostly mechanistic ecohydrological simulations from
662 20 available flux tower sites, we found that ET and GPP of SEA locations are strongly
663 energy-limited and only slightly correlated with annual precipitation. The numerical



664 experiments indicate that ET is highly responsive to changes in relative humidity for
665 tropical and subtropical regions. However, GPP is more responsive to shortwave
666 radiation changes. Warmer temperatures can decrease GPP as the plant thermal
667 optimum for photosynthesis might be exceeded and higher VPD decreases GPP due to
668 its effect on stomata closure. We quantitatively disentangle the relative effect of
669 temperature and humidity and found that the temperature effect is more substantial on
670 GPP. By integrating the flux tower observations and mechanistic modelling studies,
671 we have provided a comprehensive picture of water, energy and carbon fluxes for
672 many major ecosystems of a generally understudied and diverse region as SEA.
673 Spatial heterogeneity within SEA remains evident, and while tropical and subtropical
674 evergreen forests are dominant (~40%), ecoregions such as grasslands in the Tibetan
675 plateau, savannas, and dry deciduous forests occupy ~33% of SEA and behave quite
676 differently, as water-limitations have an important role in their functioning. This study
677 provides deeper insights into the magnitude and environmental factors affecting
678 ecohydrological fluxes across SEA, contributing knowledge to how carbon and water
679 cycle dynamics might change under a future climate.

680 **Code and data availability statement**

681 The reconstructed landcover of Southeast Asia for year 2022 are available in Zenodo:

682 <https://doi.org/10.5281/zenodo.16525412> The T&C model code is available at the

683 following link: <https://codeocean.com/capsule/0294088/tree/v4>.

684 **Author contributions**

685 JR and SF conceived the research idea and designed the study. JR, ZL, and SF
686 collected the data. JR and SF performed model simulations. All authors contributed to
687 the discussion and interpretation of the results. JR led the writing of the manuscript
688 with help from all authors. SF, XL, and SG initiated the projects.



689 **Competing interests**

690 The authors declare that they have no conflict of interest.

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