Full title

Variation of climate and its temporal shifts across an altitudinal gradient of tropical rainforests of Sri Lanka

Short title

Climate and its temporal shifts in tropical rainforests of Sri Lanka

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Abstract

Climate and its variability strongly influence the structure and dynamics of tropical rainforests, a biome which is critical for regulation of the global climate. We characterized the climate of a series of rainforest plots in Sri Lanka across a wide altitudinal range (117 to 2132 m above sea level) during 1990-2018 and determined its temporal shifts from the climate of 1961-1989. Long-term (1961-2018) climatic data were obtained from WorldClim2 and CRU-TS-4.03 global databases. Soil water deficit was computed, on a monthly (SWD) and cumulative (CSWD) basis, as the difference between rainfall and evapotranspiration using a validated model. During 1990-2018, decreases with altitude were faster in annual mean minimum temperatures (T_{min}) than in annual mean maximum temperature (T_{max}). The diurnal temperature range (DTR) increased with altitude. Within-year variation patterns of T_{max}, T_{min} and DTR were different, with peaks in March, April-May, and April respectively. Forests at higher altitudes experienced greater DTRs with greater within-year fluctuation than those at mid- and lower altitudes. Long-term annual rainfall and solar irradiance decreased while SWD and CSWD increased with increasing altitude. All altitudes showed peak SWD and CSWD in February-March. The higher altitudes showed an additional peak in June-July. Inter-annual variability, quantified in terms of the coefficient of variation, was greater for rainfall than for temperature, while CSWD and SWD showed the highest variability. Annual mean T_{max} and T_{min} increased with time during both periods. Annual total R_F decreased with time during 1961-1989, but did show a significant trend during 1990-2018. Consequently, maximum monthly SWD and CSWD decreased from 1961-1989 to 1990-2018. The Dry-Season Index, defined as the annual maximum CSWD, increased during 1961-1989, but decreased during 1990-2018. Altitudinal trends of climatic variables show that the requirement of adaptive mechanisms for climate variability is greatest in montane forests at high altitudes.

Keywords: Climate variability, Diurnal temperature range, Maximum temperature, Minimum temperature, With-year variation

Introduction

Tropical rainforests of Sri Lanka play crucial roles in the island's carbon and water cycles, environmental sustenance, and biodiversity conservation [1–3]. Long-term climate change, both at the global scale [4] and the local scale [5], can exert significant impacts on the ecosystem services of tropical rainforests [6] and tropical rainforests of Sri Lanka (TRFSLs) [7]. However, the climate experienced by TRFSLs is poorly characterized and there are only a few previous studies on this important aspect that could exert a crucial influence on their future management and sustenance [8–10]. Furthermore, the few published studies provide contradictory conclusions. For example, Hapuarachchi et al.[9] analyzed long-term rainfall and air temperature data from 1866 to 2021 at four altitudes from 477 m to 1880 m within three TRFSLs (*viz.* Knuckles, Peak Wilderness and Horton Plains) and found significant increasing trends for temperature and decreasing trends for annual rainfall. On the other hand, in an analysis of 30-year rainfall data from four stations around the Sinharaja Man and Biosphere Forest Reserve, Samarasinghe et al. [10] found no significant long-term trend. Furthermore, land surface temperatures estimated from remotely sensed Landsat satellite images in the Sinharaja forest showed both increases and decreases at different time points from 1992 to 2019. Differences in the spatial and temporal scales and the analytical methodologies of these studies probably contributed to their contrasting conclusions. More comprehensive analyses of long-term rainfall trends across Sri Lanka, without specifically focusing on rainforest sites, have shown both increases and decreases at different locations and rainfall seasons [11–15].

Tropical rainforests of Sri Lanka are predominantly located in its South-West and the Central Highlands, which experience a well-distributed annual rainfall regime in excess of 1800 mm.

However, TRFSLs experience a wide range of temperature regimes as they span across a wide altitudinal range from lowland evergreen forests at the lower altitudes (*ca.* < 800 m above mean sea level) to lower- and upper montane forests at the mid- (*ca.* 800 – 1600 m) and higher (*ca.* > 1600 m) altitudes. Therefore, variations in temperature could interact with rainfall variations, and exert a substantial influence on the functioning, productivity, structure, species composition and biodiversity of TRFSLs [16], in accordance with similar effects observed globally [17,18]. However, characterization of the gradients of key climatic variables across the range of altitudes at which TRFSLs occur has not been done so far. Therefore, this work addresses a crucial information gap to enable establishment of climate-vegetation relationships across TRFSLs in subsequent studies.

Variation of climate along altitude gradients include both variations which are directly linked to altitude and those that are not directly linked to altitude [19]. The first category includes temperature, atmospheric pressure and partial pressure of gases such as oxygen and carbon dioxide, clear sky radiation and the fraction of UV-B radiation. The second category includes rainfall, cloudiness, incident solar irradiance, relative humidity, wind characteristics and seasonality of climate. These two categories of climatic variables and their interaction with land surface characteristics such as topography, slope and aspect combine to create unique environmental gradients across specific altitudinal ranges where tropical rainforests occur. Therefore, there is a need to characterize the variation patterns of key climatic variables across the range of altitudes traversed by the TRFSLs.

Availability of water in the soil is a key environmental variable that determines the primary productivity of TRFs. Despite being in relatively high rainfall environments, tropical rainforests are highly sensitive to drought in terms of their photosynthesis, canopy greenness, light use efficiency, wood growth and net primary productivity [20–22]. Droughts occurring at a frequency of 1 -3 episodes per decade, most of which are triggered by phenomena such as El-Niño Southern Oscillation (ENSO), have caused substantial tree mortality in major tropical forests such as the Amazon [23–26]. Drought is induced by soil water deficits as a result of evapotranspiration exceeding rainfall over a prolonged period. Therefore, it is important to determine the magnitude of potential maximum soil water deficits that are likely to develop across the range of altitudes occupied by the TRFSLs.

In this work, our objective was to characterize the climate across the altitude range of TRFSLs and its temporal shifts across two 30-year time spans, viz. from 1961-1989 to 1990-2018. As determination of altitudinal gradients of key climatic variables of TRFSLs have not been done this work addresses a crucial information gap to enable establishment of climate-vegetation relationships across this crucial ecosystem in Sri Lanka. It will also provide a rational basis for formulation of policies and action plans to ensure conservation of TRFSLs in the face of climate change.

Materials and Methods

Establishment of permanent sampling plots in tropical rainforests

Ten one-hectare permanent sampling plots (PSPs) were established in tropical rainforests across an increasing altitudinal gradient in Sri Lanka as part of a multidisciplinary research project to monitor their long-term response to climate change. The PSPs traversed an altitude range from 117 m to 2132 m above sea level. Forests having an extent greater than 100 ha and showing minimum or no evidence of large-scale natural disturbance or human interference during the past three decades or longer were selected when establishing PSPs. The altitude range was divided into five class intervals, *viz.* 0-400 m, 400-800 m, 800-1200 m, 1200-1800 m and above 1800 m and at least two PSPs were established within each interval. Locations and geographic details of the PSPs are given in Fig 1 and Table 1. Key vegetation and soil characteristics of the rainforests in the PSPs are described in Sanjeewani et al. [16,27].

Fig 1. Location of permanent sampling plots in tropical rainforests across the altitudinal gradient in Sri Lanka. Kanneliya Plot 1 (KDN1 at 117 m above mean sea level), Kanneliya Plot 2 (KDN2 - 174 m), Sinharaja-Pitadeniya Plot 1 (PTD1 - 509 m), Sinharaja-Pitadeniya Plot 2 (PTD2 - 618 m), Sinharaja-Enasalwatte Plot 1 (ENS1 – 1042 m), Enasalwatte Plot 2 (ENS2 – 1065 m), Rilagala (RLG - 1668 m), Hakgala (HKG -1804 m), Piduruthalagala (PTG - 2080m) and Horton Plains (HNP – 2132 m).

Table 1. Geographic details of the ten permanent sampling plots in tropical rainforests of Sri Lanka

PSP[†]	Agro-Ecological region[‡]	Altitude class (m)	Mean altitude (m asl)	Latitude (°N)	Longitude (°E)	Forest Type*
KDN1	WL1a	0-400	117	6.24749	80.34071	TLF
KDN2	WL1a	0-400	174	6.26090	80.35191	TLF
PTD1	WM1a	400-800	509	6.39633	80.47070	TLF
PTD2	WM1a	400-800	618	6.38141	80.47786	TLF
ENS1	WU1	800-1200	1042	6.39433	80.59709	TLMF
ENS2	WU1	800-1200	1065	6.39439	80.59565	TLMF
RLG	WU1	1200-1800	1668	6.97619	80.58330	TMF
HKG	WU3-IU3d	1200-1800	1804	6.92725	80.81839	TMF
PTG	WU3-IU2	Over 1800	2080	6.98197	80.77276	TMF
HNP	WU3-IU3b	Over 1800	2132	6.81459	80.80421	TMF

[†]PSP – Permanent Sampling Plots;
[‡]Based on Punyawardena et al. [28]. WL - Low Country Wet zone; WM – Mid Country Wet Zone; WU – Up Country Wet Zone; IU – Up Country Intermediate Zone. TLR - Tropical Lowland rainforest; TLMF- Tropical Lower montane forests; TMF - Tropical Montane Forest.
*Based on Gunatilleke et al. [29].

Acquisition of climatic data

Climatic data were obtained from the global climatic databases WorldClim 2 [30] and CRU-TS-4.03, bias corrected with WorldClim 2.1 [31]. These databases contain spatially interpolated historical climatic data at a resolution of approximately 21 km^2 (1961-2018) and 1 km^2 (1970-2000). The databases consist of monthly averages of mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) air temperatures, daily solar irradiance, vapour pressure and wind speed and monthly total rainfall (R_F).

Rationale for determining the time scale of climatic data

Rainforests of the present study have remained undisturbed for three decades or longer. As such their present status has been determined by the climate experienced over a similar time scale. Size of the foliage canopy is a major determinant of the functioning and productivity of tropical forests [32–34]. It is controlled by the rates of leaf initiation (i.e., leaf flushing), expansion and senescence, which are influenced by the climate experienced across different time scales. The 'recent' climate experienced within the past decade most likely determined the rates of leaf initiation, expansion and senescence as these processes are strongly influenced by the sum of thermal time experienced and the availability of light and water [35]. On the other hand, the number of leaves that initiate and expand at any given time is controlled by the number of buds that are initiated, and the amount of assimilates (i.e., stored reserves) available for leaf growth [36]. The number of flushing points and stored reserves are, most likely, determined by the accumulated tree biomass, its branching pattern, and the size of the root system to acquire the resources (e.g., water, nutrients etc.) to produce tree biomass. Accumulated tree biomass is strongly dependent on the long-term climate experienced by trees in terms of solar irradiance, water availability and temperature [37]. Accordingly, in addition to the direct influence of the relatively 'recent' climate, the long-term, 'past' climate probably exerted an indirect influence on the observed vegetation status of the rainforests of the present study. Therefore, climatic data during the period from 1990 to 2018 were used to compute the mean climate that has determined their present status. On the other hand, mean climate during the period from 1961 to 1989 was used as the benchmark to determine its temporal shifts during 1990-2018.

Computation of long-term means of key climatic variables

All computations were done separately for the 1990-2018 and 1961-1989 periods. Monthly diurnal temperature range (DTR) was computed as the difference between T_{max} and T_{min} of each month. Monthly means of T_{min}, T_{max}, T_{mean} and DTR were used in computing their long-term averages for the respective PSPs. Mean annual R_F was computed by averaging the monthly totals and summing them over the respective 12-month period. As monthly means of daily solar irradiance data were available only for the 1970-2000 period, the long-term average S_R was computed by first obtaining their respective monthly means, followed by obtaining the annual mean over the 30-year period.

Computation of soil water deficit and dry season index

Soil water deficit (SWD) was computed separately for each PSP on a monthly basis for the Two periods from January 1990 to December 2018 and from January 1961 to December 1989, using the soil water deficit model of Malhi and Wright [38]. This model computes the magnitude and duration of soil water deficit while taking in to account the soil water status at the beginning of each month of computation. An initial SWD_i for each month *i* was computed as the difference between its rainfall (Rf_i) and evapotranspiration (Et_i),

$$SWD_i = Rf_i - Et_i \quad (1)$$

Evapotranspiration was estimated by the following equation developed by Malhi *et al.* [39] and used in Malhi and Wright [38],

$$Et_i = (a \times SWD_i) + Et_o \quad (2)$$

where, Et_o is the potential evapotranspiration in the absence of soil water deficits and *a* is a coefficient of drought sensitivity of evapotranspiration. Based on the work of Shuttleworth [40] and Malhi *et al.* [39], values of 118 mm $month^{-1}$ and -0.3625 were used by Malhi and Wright [38] for Et_o and *a* respectively. A review of measured or estimated Et of TRFs in different continents (i.e. Asia, South America and Africa) in published literature (S1 Table) provided a strong validation for using the above values as coefficients of equation 2.

After calculating the SWD_i for the initial month of each period (i.e., January 1961 and 1990), SWD for each successive month (SWD_{i+1}) was computed as,

$$SWD_{i+1} = SWD_i + Et_{i+0.5} - Rf_{i+0.5} \quad (3)$$

where, $Et_{i+0.5}$ and $Rf_{i+0.5}$ were the mean Et and Rf of the successive months *i* and *i+1*. Use of the mean Et and Rf takes in to account the variation of daily Et and Rf during the month *i+1*. This computation assumes that daily Et and Rf varies linearly during the period between the two successive months.

If $Rf_{i+0.5}$ exceeds (SWD_i + $Et_{i+0.5}$), then soil becomes saturated and SWD_{i+1} is set to zero. If $Rf_{i+0.5}$ is less than (SWD_i + $Et_{i+0.5}$), then SWD_{i+1} is added to SWD_i to obtain the cumulative SWD (CSWD). This process was repeated for each successive month up to December of 1989 and 2018 using the monthly rainfall data. The annual maximum CSWD in a given year in a given site was identified as a dry-season index (DSI) by Malhi and Wright [38].

Statistical analysis

Determination of altitudinal trends of annual mean climatic variables

All statistical analyses were done on Statistical Analysis System (SAS) [41]. Normality of the distributions of monthly means of T_{max}, T_{min}, T_{mean}, DTR and R_F was tested separately for each PSP and the two periods using Proc Univariate in SAS. Monthly means of climatic variables (T_{max}, T_{min}, T_{mean}, DTR, R_F and S_R) and soil water deficits (monthly SWD and CSWD) and standard errors of the monthly means were computed. Variation of the monthly means of climatic and soil variables with altitude was determined by linear regression analysis. Variability of the climatic and soil variables over each period was quantified as the coefficient of variation of their respective monthly means. Variation of long-term annual means with altitude was determined by linear regression. Maximum monthly means of SWD (SWD_{max}) and CSWD ($CSWD_{max}$) observed in the respective PSPs were regressed against altitude to determine their rate of change with altitude.

Determination of temporal shifts in long-term climatic variables

The long-term temporal trends of annual mean T_{max} and T_{min}, annual total R_F and annual DSI and their possible shifts over time were determined using the following procedure, which was applied to each PSP separately. If the annual means of temperatures, annual totals of R_F and annual DSI in each PSP were normally distributed, an initial linear regression analysis was done to determine their respective temporal trends. If the annual means or totals deviated from normality, their temporal trends were determined by the Mann-Kendall test [42]. After the initial linear regression on the normally distributed annual means or totals, the randomness of residuals was tested by the Runs test of randomness using the Wald-Wolfowitz statistic [43]. The independence of residuals was tested by the Durbin-Watson test [44]. If the residuals satisfied the condition of randomness, the linear regression slope was considered as the rate of change of the annual mean or total with time. If the residuals satisfied the condition of independence, the confidence interval of the regression slope was used to determine whether the slope was significantly different from zero. If the residuals of the initial linear regression deviated from normality, the temporal trend was determined by the Mann-Kendall test. The above analysis was carried out separately for the periods from 1961 to 1989 (Period 1) and from 1990 to 2018 (Period 2) to determine possible shifts in temporal trends with time.

In order to determine their shifts with time, mean monthly SWD and CSWD that were computed for the two periods (both spanning a duration of 29 years) were compared for significance of their difference using the paired t-test. Similarly, the maximum monthly SWD and CSWD (SWD_{max}

and $CSWD_{max}$) observed during each of the 29-year period for each PSP were compared using the paired t-test to detect significant shifts with time.

Results

Variation of climate of tropical rainforest plots across the altitudinal gradient during the 1990-2018 period

Annual means of T_{min}, T_{max} and T_{mean} and annual total R_F were normally distributed in all PSPs (Results not shown). However, the corresponding distributions of DTR deviated significantly ($P<0.05$) from normality. As expected, the long-term means of T_{min}, T_{max} and T_{mean} of PSPs decreased with increasing altitude (Table 2). In contrast, long-term mean DTR showed an increasing trend with increasing altitude. Accordingly, there was a 2.5°C difference between the PSPs with the highest (Pidurutalagala) and the lowest (Plot 1 in Kanneliya) long-term mean DTR. Although the annual total R_F showed an overall decreasing trend with altitude (Table 3) there were a few notable exceptions to this trend. These include plot 1 in Kanneliya (KDN1) and Pidurutalagala, both of which have lower R_F than the PSPs which are at the next higher altitude (i.e., Plot 2 in Kanneliya and Horton Plains). It can be noted that both plots in Sinharaja-Enasalwatte (ENS1 and ENS2) have experienced the same climate as both are located close together.

Table 2. Means and standard errors of key temperature variables of the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient during the 1990-2018 period.

PSP	Alt. (m)	T_{min} (°C)	SE[†] (°C)	T_{max} (°C)	SE (°C)	T_{mean} (°C)	SE (°C)	DTR (°C)	SE (°C)
KDN1	117	23.53	0.248	29.24	0.240	26.38	0.237	5.71	0.115
KDN2	174	23.10	0.248	28.96	0.240	26.03	0.237	5.86	0.118
PTD1	509	20.78	0.250	27.01	0.241	23.90	0.238	6.23	0.121
PTD2	618	20.78	0.250	27.01	0.241	23.90	0.238	6.23	0.121
ENS1	1042	18.46	0.249	25.13	0.240	21.80	0.238	6.68	0.114
ENS2	1065	18.46	0.249	25.13	0.240	21.80	0.238	6.68	0.114
RLG	1668	16.59	0.260	24.68	0.247	20.63	0.240	8.08	0.163
HKG	1804	13.01	0.256	21.05	0.244	17.03	0.240	8.04	0.142
PTG	2080	11.60	0.257	19.82	0.245	15.71	0.240	8.22	0.148
HNP	2132	11.15	0.254	19.19	0.244	15.17	0.240	8.04	0.133

Alt. – Altitude; T_{max}, T_{min} and T_{mean} –Annual maximum, minimum and mean air temperatures; DTR – Diurnal temperature range; [†]SE – Pooled standard error of mean calculated after pooling the monthly variances.

Table 3. Means and standard errors of rainfall (1990-2018) and incident solar radiation (1970-2000) of the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

PSP	Alt. (m)	R_F (mm y^{-1})	SE (mm y^{-1})	S_R (MJ m^{-2} d^{-1})	SE (MJ m^{-2} d^{-1})
KDN1	117	3677	103	18.945	0.449
KDN2	174	3938	110	18.833	0.437
PTD1	509	3922	109	18.496	0.425
PTD2	618	3922	109	18.330	0.430
ENS1	1042	3160	87	17.910	0.437
ENS2	1065	3160	87	17.910	0.437
RLG	1668	3043	84	17.731	0.471
HKG	1804	2034	56	17.688	0.476
PTG	2080	1926	53	17.460	0.477
HNP	2132	2069	56	17.398	0.478

Alt. – Altitude; R_F – Total annual rainfall (1990-2018); S_R – Daily solar irradiance (1970-2000); SE – Pooled standard error of mean.

Within-year variation of average climate during the 1990-2018 period

At all altitudes, monthly mean maximum temperature (T_{max}) showed an increasing trend from January to March-April (Fig 2A). This increasing trend peaked in March in the PSPs at lower (Kanneliya and Sinharaja-Pitadeniya) and mid (Sinharaja-Enasalwatte) altitudes. However, at higher altitudes (Hakgala, Pidurutalagala and Horton Plains) the increasing trend in T_{max} continued up to April. At the lower and mid altitudes, T_{max} declined from April onwards to reach a lower plateau during the three-month period from July to September. At higher altitudes, T_{max} remained high in May also, but showed sharp decline in June to a lower plateau from June to August. At lower and mid altitudes, T_{max} showed a very slow increasing trend from September onwards. This increasing trend accelerated in January. At higher altitudes, a sharp increase in T_{max} could be observed from August to September, which was followed by a very slow decreasing trend from September to November. The variation pattern of T_{max} in Rilagala at an altitude of 1668 m was closer to the corresponding pattern in Sinharaja-Enasalwatte (altitude 1042-1065 m) than to the pattern in Hakgala (1804 m).

Fig 2. Variation of monthly mean maximum temperature (A) and minimum temperature (B) during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient. Error bars indicate the standard error of means.

The variation pattern of long-term average monthly minimum temperature (T_{min}) (Fig 2B) was different from that of T_{max}. At lower altitudes (i.e., Kanneliya and Sinharaja-Pitadeniya), T_{min} showed a continuous increase from January to May before declining slowly until December. At the mid and higher altitudes, T_{min} increased from February to a peak in June, which was followed by a decline till January in the following year. Both the increases and the decreases of T_{min} were sharper (i.e., at higher rates) in the mid and higher altitudes than at the lower altitudes.

The within-year variation of long-term average monthly mean temperature (T_{mean}) showed a single peak (Fig 3A). At the lower altitudes, this peak occurred in April whereas at the mid and higher altitudes, it occurred in May. Following a decline from the peak, T_{mean} at all altitudes remained stable during the four-month period from July to October before beginning the declining period from October to January.

Fig 3. Variation of monthly mean average temperature (A) and diurnal temperature range (B) during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

The day-night temperature differential, as quantified by the diurnal temperature range (DTR), showed a peak in the February-April period and a trough in the June-August period (Fig 3B). Throughout the year, DTR in the four higher altitude sites (i.e., Rilagala, Hakgala, Pidurutalagala and Horton Plains) was greater than that in the mid and lower altitude sites. Furthermore, the difference between periods of the highest and lowest DTR was highest in the four high altitude sites, being between 5.55°C (Rilagala) and 6.23°C (Pidurutalagala). The corresponding value in the mid altitude site at Sinharaja-Enasalwatte was 4.27°C. The lower altitude sites of Sinharaja-Pitadeniya and Kanneliy recorded differences of 3.92°C and 3.42°C between the months of the highest and lowest DTR.

Monthly total rainfall (R_F) patterns were different between the lower and higher altitudes (Fig 4). The overall patterns at the lower and mid altitudes were clearly bimodal with two prominent and approximately equal peaks, whereas the higher altitudes had only one prominent peak and a minor peak. At lower altitudes (Kanneliya and Sinharaja-Pitadeniya), the peaks occurred in May where R_F exceeded 450 mm month^{-1} and in October-November where R_F exceeded 400 mm month^{-1}. The mid (Sinharaja-Enasalwatte) and higher-mid (Rilagala) altitudes also had their R_F peaks in May and November, which at 300 - 400 mm month^{-1}, were lower than the respective peaks of the low altitudes. At high altitudes, the single prominent R_F peak occurred in November with around 250 mm month^{-1} while the minor peak that occurred in April had only 150 - 170 mm month^{-1}. It is notable that among these high-altitude sites, Horton Plains showed an additional R_F peak in August, with 235 mm month^{-1}. Except during the December-January period, monthly totals R_F of lower and mid altitudes were always greater than those of the corresponding months at higher altitudes.

Fig 4. Variation of monthly total rainfall during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

Daily irradiance (S_R) also showed a bimodal variation pattern at all altitudes (Fig 5). One peak occurred in March while the other occurred in August - September. During the peak in March, S_R showed a clear decreasing trend with increasing altitude. The highest S_R (22.30 MJ m^{-2} d^{-1}) was in Kanneliya-Plot 1 whereas the lowest (20.62 MJ m^{-2} d^{-1}) was in Horton Plains. The Sr peak in August-September was slightly lower (*ca.* 18 - 19 MJ m^{-2} d^{-1}) than that in March. Furthermore, there was no clear variation pattern of S_R with altitude during this peak. In between these two peaks, two prominent troughs were also evident, one in June and the other December. During both these periods, S_R showed decreasing trends with increasing altitude, within ranges of 14.97 - 16.97 MJ m^{-2} d^{-1} and 15.73 - 17.26 MJ m^{-2} d^{-1}during June and December respectively.

Fig 5. Variation of monthly mean daily solar irradiance during the period from 1970 to 2000 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

Within-year variation of monthly soil water deficit during the 1990-2018 period

Variation patterns of the monthly soil water deficit (SWD) and the cumulative soil water deficit (CSWD) showed clear separation based on altitude (Fig 6). Table 4 shows the maximum values of long-term monthly mean SWD and CSWD observed in each PSP and the months during which these maxima occurred.

Fig 6. Variation of monthly mean soil water deficit (A) and cumulative soil water deficit (B) during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

Monthly soil water deficit (SWD) was highest during the February-March period at all altitudes (Fig 6A, Table 4). This was followed by a reduction of SWD from March to April. During the rest of the year from May to December, SWD remained below 5 mm $month^{-1}$ at all altitudes below 1800 m. At altitudes greater than 1800 m, the reduction of SWD from March to April did not reach as low as at altitudes lower than 1800 m. Thereafter, the three highest altitudes experienced another increase of SWD from May to June. Even though the SWD decreased from June to August, it was higher than the corresponding SWDs at altitudes lower than 1800 m during the same period. There was another smaller increase of SWD from August to September at the three highest altitudes, which was followed by a continuous reduction from September to December.

Table 4. Maximum mean monthly soil water deficit (SWD_{max}) and cumulative SWD ($CSWD_{max}$) observed during the period from 1990 to 2018 in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

PSP	Alt. (m)	SWD_{max} (mm month^{-1})	SE (mm month^{-1})	Month observed	$CSWD_{max}$ (mm)	SE (mm)	Month observed
KDN1	117	11.94	5.42	February	21.05	10.98	March
KDN2	174	10.92	5.17	February	18.50	10.04	March
PTD1	509	11.18	5.20	February	15.85	9.57	March
PTD2	618	11.18	5.20	February	15.85	9.57	March
ENS1	1042	25.48	6.65	February	36.92	9.66	February
ENS2	1065	25.48	6.65	February	36.92	9.66	February
RLG	1668	21.98	6.04	February	36.34	13.99	March
HKG	1804	40.54	7.54	March	72.56	14.64	March
PTG	2080	53.97	7.66	March	92.14	15.28	March
HNP	2132	51.22	7.99	March	106.26	17.23	March

Alt. – Altitude; SE – Standard error.

The maximum monthly SWD experienced in March was highest at the two highest altitudes (Pidurutalagala and Horton Plains), with the next highest altitude (Hakgala) also showing a substantially higher SWD than the altitudes lower than 1800 m (Table 4). The altitudes below 1800 m experienced the maximum monthly SWD in February. The maximum SWDs at the mid- (Sinharaja-Enasalwatta) and higher-mid (Rilagala) altitudes were lower than the maxima of the highest altitudes but were higher than the maxima of the lower-mid (Sinharaja-Pitadeniya) and the lowest (Kanneliya) altitudes. Among the three highest altitudes, which showed smaller peaks of monthly SWD in June and September, Hakgala and Pidurutalagala experienced greater SWDs than Horton Plains.

Within year variation of cumulative soil water deficit during the 1990-2018 period

The within year variation of cumulative soil water deficit (CSWD) among the different altitudes (Fig 6B) showed a similar pattern of variation to that of monthly SWD (Fig 6A). The CSWD reached maximum in March at all altitudes except the mid-altitude in Sinharaja-Enasalwatte, where CSWD peaked in February (Table 4). The three highest altitudes experienced two further, smaller peaks in June (Horton Plains)-July (Hakgala and Pidurutalagala) and September. During March, the highest CSWD of 106 mm was observed at the highest altitude in Horton Plains. This was followed by the next higher altitudes, Pidurutalagala (92 mm) and Hakgala (73 mm). The maximum CSWD of altitudes below 1800 m were substantially lower than those at altitudes above 1800 mm.

Variation of monthly mean climatic variables and soil water deficit with altitude during the 1990-2018 period

As expected, all monthly means of T_{max}, T_{min} and T_{mean} showed highly significant ($P<0.0001$) linear reductions with increasing altitude (Table 5). Rates of reduction of T_{min} of all months were greater than the corresponding rates of reduction of T_{max}. Consequently, the respective reduction rates of T_{mean} were intermediate to those of T_{max} and T_{min}. The respective rates of reduction of the three temperature variables showed variation among different months of the year. January, December and June showed the highest rates of reduction for T_{max} whereas May, April and September showed the lowest rates. March, February and January showed the highest rates of reduction of T_{min} while June, July and November showed the lowest. The highest rates of reduction of T_{mean} were in February, January and March while the lowest rates of in May, September and October. In contrast to the three temperature variables, the diurnal temperature range (DTR) of all months increased

($P<0.0001$) with increasing altitude. The rate of increase was highest in March, April and May and was lowest in June, July and November.

Table 5. Change of monthly means of key climatic variables with altitude during the period from 1990 to 2018 in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

Month	Change (°C per 1000 m increase in altitude)							
	T_{max}	Adj. R^2	T_{min}	Adj. R^2	T_{mean}	Adj. R^2	DTR	Adj. R^2
January	-4.889^{***}	0.928	-6.084^{***}	0.969	-5.486^{***}	0.953	1.194^{***}	0.922
February	-4.574^{***}	0.909	-6.441^{***}	0.967	-5.508^{***}	0.947	1.867^{***}	0.948
March	-4.365^{***}	0.909	-6.539^{***}	0.965	-5.452^{***}	0.946	2.175^{***}	0.970
April	-4.150^{***}	0.918	-6.209^{***}	0.963	-5.179^{***}	0.947	2.058^{***}	0.977
May	-4.014^{***}	0.926	-5.953^{***}	0.963	-4.984^{***}	0.950	1.939^{***}	0.983
June	-4.863^{***}	0.932	-5.442^{***}	0.958	-5.152^{***}	0.947	0.579^{***}	0.855
July	-4.794^{***}	0.930	-5.476^{***}	0.958	-5.135^{***}	0.946	0.682^{***}	0.914
August	-4.736^{***}	0.932	-5.569^{***}	0.961	-5.152^{***}	0.948	0.833^{***}	0.938
September	-4.292^{***}	0.923	-5.834^{***}	0.963	-5.063^{***}	0.948	1.543^{***}	0.967
October	-4.563^{***}	0.926	-5.588^{***}	0.964	-5.075^{***}	0.949	1.025^{***}	0.897
November	-4.762^{***}	0.931	-5.495^{***}	0.960	-5.129^{***}	0.948	0.733^{***}	0.805
December	-4.832^{***}	0.939	-5.756^{***}	0.967	-5.294^{***}	0.956	0.924^{***}	0.913

T_{max}, T_{min} and T_{mean} – Maximum, minimum and mean air temperatures; DTR – Diurnal temperature range; *** – Significant at $P<0.0001$.

Monthly mean R_F in January and July did not show a significant ($P>0.05$) trend with altitude. However, all other months showed significant ($P<0.05$) reductions in their mean R_F with increasing altitude (Table 6). May, March and October showed the highest rates of reduction while December, February and August showed the lowest. Monthly SWD and CSWD showed significant ($P<0.05$) linear increases with altitude in seven out of the 12 months. January, August, October, November and December were the months which did not show significant ($P>0.05$) trends with altitude. Among the months in which SWD and CSWD increased significantly ($P<0.05$) with altitude, their respective rates of increase were highest in March and lowest in September. It was notable that April also had a higher rate of increase for CSWD which was close to the maximum observed in March.

Table 6. Change of monthly means of rainfall and soil water deficit with altitude during the period from 1990 to 2018 in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

Month	Change (mm per 1000 m increase in altitude)								
	R_F	Adj. R^2	P	SWD	Adj. R^2	P	CSWD	Adj. R^2	P
January	-14.31	0.051	ns	1.398	-0.040	ns	1.115	-0.086	ns
February	-50.19	0.896	<0.0001	13.49	0.784	0.0004	16.65	0.640	0.0033
March	-120.29	0.817	0.0002	22.17	0.764	0.0006	39.09	0.747	0.0008
April	-110.17	0.838	0.0001	8.109	0.688	0.0018	35.05	0.735	0.0009
May	-165.07	0.910	<0.0001	4.968	0.708	0.0014	5.827	0.694	0.0017
June	-102.49	0.677	0.0021	9.911	0.558	0.0079	15.92	0.622	0.0041
July	-25.91	0.168	ns	5.014	0.339	0.0453	13.82	0.421	0.0252
August	-69.17	0.563	0.0075	1.666	0.274	ns	3.000	0.234	ns
September	-72.11	0.837	0.0001	3.837	0.482	0.0156	5.211	0.433	0.0229
October	-120.43	0.887	<0.0001	0.193	0.237	ns	0.536	0.243	ns
November	-101.57	0.827	0.0002	.[†]	.	.	.	.	.
December	-43.75	0.542	0.0091	-0.143	-0.107	ns	-0.143	-0.107	ns

R_F – Rainfall; SWD – Soil water deficit; CSWD – Cumulative SWD; ns – Non-significant at P=0.05. [†]The SWD and CSWD in November was zero at all altitudes.

Variation of annual means of climate and maximum soil water deficit with altitude during the 1990-2018 period

Long-term annual means of all climatic variables (Tables 2 and 3) and maximum soil water deficits (Table 4) showed highly significant ($P < 0.001$) linear relationships with altitude (Table 7). All three temperature variables, R_F and S_R decreased whereas DTR, SWD_{max} and $CSWD_{max}$ increased with increasing altitude. Similar to the corresponding variations in their monthly means (Table 5), annual mean T_{min} showed a greater change with altitude than T_{max}.

Table 7. Change of annual means of key climatic variables and maximum soil water deficits with altitude during the period from 1990 to 2018 in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

Variable	Change per 1000 m increase in altitude	Adj. R^2	P
T_{max} (°C)	-4.57	0.926	<0.0001
T_{min} (°C)	-5.87	0.964	<0.0001
T_{mean} (°C)	-5.22	0.949	<0.0001
DTR (°C)	1.30	0.955	<0.0001
R_F (mm y^{-1})	-995	0.855	<0.0001
S_R (MJ m^{-2} d^{-1})	-0.698	0.928	<0.0001
SWD_{max} (mm $month^{-1}$)	20.01	0.817	0.0002
$CSWD_{max}$ (mm)	38.86	0.774	0.0005

T_{max}, T_{min} and T_{mean} – Maximum, minimum and mean air temperatures; DTR – Diurnal temperature range; R_F – Rainfall; S_R - Daily solar irradiance; SWD_{max} – Maximum soil water deficit; $CSWD_{max}$ – Maximum cumulative SWD.

Variability of climate and soil water deficit during the 1990-2018 period

Variability of the three temperature variables (i.e., T_{max}, T_{min} and T_{mean}) of all months of the year, as quantified in terms of their coefficient of variation (CV), increased with increasing altitude (Figs 7 and 8A). The rate of increase of CV with altitude was smaller at altitudes up to 1668 m. There was a distinct rise in the rate of increase of CV of the temperatures from 1668 m to 2080 m. Consequently, CVs of all three temperature variables were higher at altitudes above 1668 m than at altitudes below 1668 m. In general, CVs of T_{min} were greater than those of T_{max} with T_{mean} showing intermediate CVs. The CV of T_{max} was highest in April at altitudes up to 1668 m while June had the highest CV at altitudes above 1668 m (Fig 7A). August had the lowest CV in T_{max} across the whole range of altitudes. March and April showed the highest CVs in T_{min} whereas August and November showed the lowest CVs at all altitudes (Fig 7B).

Fig 7. Altitudinal variation of the coefficient of variation (CV) of monthly maximum temperature, T_{max}, (A) and minimum temperature, T_{min}, (B) during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

Fig 8. Altitudinal variation of the coefficient of variation (CV) of monthly mean temperature, T_{mean}, (A) and diurnal temperature range, DTR, (B) during the period from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

The CV of T_{mean} was highest in April while being lowest in August and September (Fig 8A). The CV of DTR showed a different variation pattern (Fig 8B) to those of the three temperature variables. All months showed a slow decrease in CV from the lowest (117 m) to mid altitudes (1042 m and 1065 m), followed by an increase up to 1668 m and clear decreases from 1668 m to 1804 m and from 2080 m to 2132 m. March showed the highest CV while April showed the lowest CV for DTR across the whole range of altitudes.

Rainfall showed a much greater range of CV, i.e., 30 – 76%, (Fig 9A) than the four temperature variables, i.e., 1 – 6%, (Figs 7 and 8). On the other hand, except in June, CV of R_F did not show appreciable variation across different altitudes. In June, CV of R_F showed an increase from mid-altitudes up to 1668 m.

Fig 9. Altitudinal variation of the coefficient of variation (CV) of monthly rainfall, R_F, (A), soil water deficit, SWD, (B) and cumulative soil water deficit, CSWD, (C) during the period

from 1990 to 2018 in permanent sampling plots of tropical rainforests in Sri Lanka across an altitudinal gradient.

In comparison to all the climatic variables, monthly SWD and CSWD had substantially higher CVs which also showed fluctuations across altitudes (Figs 9B and C). January to March showed relatively lower CVs while December showed a consistently higher CV across all altitudes. May, August and September showed high CVs from the lowest altitude up to 1668 m, followed by a substantial decrease from 1668 m to 1804 m. July showed intermediate levels of CVs from the lowest to mid-altitudes, followed by an increase from mid-altitudes to 1668 m and a decrease from 1668 m to 1804 m.

Temporal trends and their shifts with time

Mean annual maximum (T_{max}) and minimum (T_{min}) temperature

The distributions of T_{max} and T_{min} in all PSPs of both periods (i.e. 1961-1989 and 1990-2018) satisfied the condition of normality. Initial linear regressions with time showed highly significant positive linear trends during both periods ($P<0.0001$ and $P<0.01$ for 1961-1989 and 1990-2018 respectively). The residuals of linear regressions of both T_{max} and T_{min} in all PSPs for both periods were normally distributed and satisfied the Runs test for randomness based on the Wald-Wolfowitz test for randomness. All residuals of T_{max} satisfied the Durbin-Watson test for independence (i.e. the absence of autocorrelation) in all PSPs for both periods. Accordingly, the regression slopes and their confidence intervals (Table 8) represent the rates of T_{max} increase. While the rates of increase of T_{max} did not vary significantly ($P<0.05$) among the different PSPs, the rate of T_{max} increase during the 1961-1989 period was greater than that during 1990-2018 in all PSPs.

Table 8. Slopes of linear regressions of annual mean maximum temperature (T_{max}) and annual mean minimum temperature (T_{min}) during two 29-year time periods (1961-1989 and 1990-2018) in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

		T_{max} (× 10^{-2} °C y^{-1})				T_{min} (× 10^{-2} °C y^{-1})				Kendall τ (T_{min})	
PSP	**Alt (m)**	**1961-1989**	**95% CI†**	**1990-2018**	**95% CI†**	**1961-1989**	**95% CI†**	**1990-2018**	**95% CI†**	**1961-1989**	**P‡**
KDN 1	117	2.280	1.284 - 3.275	1.291	0.506 - 2.076	2.199	1.179 - 3.218	2.134	1.302 - 2.966	0.468	0.0004
KDN 2	174	2.276	1.280 - 3.272	1.281	0.495 - 2.066	2.191	1.168 - 3.214	2.149	1.314 - 2.983	0.468	0.0004
PTD1	509	2.281	1.287 - 3.275	1.283	0.491 - 2.076	2.207	1.185 - 3.229	2.172	1.330 - 3.015	0.463	0.0004
PTD2	618	2.281	1.287 - 3.275	1.283	0.491 - 2.076	2.207	1.185 - 3.229	2.172	1.330 - 3.015	0.463	0.0004
ENS1	1042	2.281	1.294 - 3.268	1.317	0.521 - 2.112	2.226	1.216 - 3.235	2.149	1.308 - 2.990	0.463	0.0004
ENS2	1065	2.281	1.294 - 3.268	1.317	0.521 - 2.112	2.226	1.216 - 3.235	2.149	1.308 - 2.990	0.463	0.0004
RLG	1668	2.325	1.306 - 3.344	1.151	0.348 - 1.954	2.227	1.154 - 3.301	2.347	1.475 - 3.218	0.443	0.0007
HKG	1804	2.317	1.316 - 3.318	1.219	0.421 - 2.017	2.258	1.212 - 3.303	2.265	1.410 - 3.119	0.463	0.0004
PTG	2080	2.323	1.318 - 3.328	1.199	0.400 - 1.999	2.251	1.198 - 3.304	2.289	1.430 - 3.148	0.463	0.0004
HTN	2132	2.317	1.321 - 3.314	1.242	0.442 - 2.043	2.257	1.226 - 3.289	2.225	1.373 - 3.077	0.468	0.0004

†95% confidence interval of the regression slope. ‡Probability of Kendall τ=0.

Although the residuals of T_{min} in all PSPs during the 1990-2018 period satisfied the Durbin-Watson test for independence, the residuals of all PSPs during the 1961-1989 period showed a positive first-order autocorrelation. The Mann-Kendall τ was significantly positive ($P<0.001$) for all PSPs during 1961-1989 (Table 8). The slopes of linear regressions of T_{min} of all PSPs during 1990-2018 were highly significant ($P<0.0001$) and positive. The corresponding regression slopes for the 1961-1989 period were also highly significant ($P<0.001$) and positive. In contrast to T_{max}, the corresponding T_{min} regression slopes of the two periods at each PSP did not differ significantly ($P>0.05$).

Annual total rainfall (R_F)

In all PSPs and both periods, R_F was normally distributed. Initial linear regressions showed significant ($P<0.05$) negative linear trends during the 1961-1989 period in all PSPs except RLG. In RLG also, the negative linear trend during 1961-1989 was significant at $P<0.1$. In contrast, during the 1990-2018 period, R_F did not show a significant ($P>0.05$) trend in any of the PSPs. During both periods, residuals of the regressions of all PSPs were normally distributed. However, the residuals of the significant linear regressions during the 1961-1989 period were not randomly distributed based on the Wald-Wolfowitz test for randomness ($P<0.05$). Furthermore, the Durbin-Watson test also showed a significant ($P<0.05$) negative first-order autocorrelation. In contrast, the residuals of regressions during the 1990-2018 period (which were not significant) satisfied the test for randomness and were not autocorrelated. The Mann-Kendall τ was negative in all PSPs during the 1961-1989 period (Table 9). In five PSPs, τ was significant at $P<0.05$ whereas in the rest it was significant at $P<0.1$.

Table 9. Mann-Kendall τ statistic for the time trends of annual total rainfall (R_F) during the period from 1961 to 1989 in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

		Kendall τ (R_F)	
PSP	**alt**	**1961-1989**	**P†**
KDN1	117	-0.286	0.0296
KDN2	174	-0.286	0.0296
PTD1	509	-0.271	0.0391
PTD2	618	-0.271	0.0391
ENS1	1042	-0.256	0.0511
ENS2	1065	-0.251	0.0557
RLG	1668	-0.217	0.0988
HKG	1804	-0.266	0.0428
PTG	2080	-0.251	0.0557
HTN	2132	-0.251	0.0557

†Probability of Kendall τ=0.

Maximum monthly soil water deficit (SWD_{max}) and cumulative maximum soil water deficit ($CSWD_{max}$)

When the monthly mean SWD and CSWD data for the two 29-year periods (i.e. 1961-1989 and 1990-2018) of all PSPs were pooled, paired t-tests showed that both SWD and CSWD had decreased significantly (P=0.0337 and 0.0082 for SWD and CSWD respectively) (data not shown). When the corresponding maxima of SWD and CSWD of PSPs were compared, monthly mean SWD_{max} showed decreases from the 1961-1989 period to the 1990-2018 period in all PSPs except Pidurutalagala (Table 10). On the other hand, $CSWD_{max}$ showed decreases from the first to the second period in all PSPs. When the data from all PSPs were pooled, paired t-tests showed these decreases to be highly significant (P=0.0004 and <0.0001 for SWD_{max} and $CSWD_{max}$ respectively).

Table 10. Maximum monthly soil water deficit (SWD_{max}) and cumulative SWD ($CSWD_{max}$) observed during the period from 1961 to 1989 and their respective changes up to the 1990-2018 period in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

		1961-1989				1990-2018	
PSP	**alt**	**SWD_{max} (mm month^{-1})**	**Std. Err. (mm month^{-1})**	**$CSWD_{max}$ (mm)**	**Std. Err. (mm)**	**Change (SWD_{max}) (mm month^{-1})**	**Change ($CSWD_{max}$) (mm)**
KDN1	117	25.42	7.21	42.25	11.56	-13.49	-21.20
KDN2	174	21.44	6.93	37.40	11.03	-10.51	-18.91
PTD1	509	22.48	6.99	38.75	11.20	-11.30	-22.90
PTD2	618	22.48	6.99	38.75	11.20	-11.30	-22.90
ENS1	1042	46.44	8.90	73.51	14.04	-20.96	-36.59
ENS2	1065	47.14	8.99	74.62	14.24	-21.66	-37.70
RLG	1668	40.70	8.30	60.25	12.92	-18.73	-23.91
HKG	1804	46.47	8.60	97.60	19.51	-5.93	-25.04
PTG	2080	52.08	8.96	123.75	20.13	1.89	-31.61
HTN	2132	62.41	9.73	131.00	21.95	-11.18	-24.74
†Paired $\|t\|$ (SWD_{max}) (df=9)			5.49 (P=0.0004)				
‡Paired $\|t\|$ ($CSWD_{max}$) (df=9)			12.97 (P<0.0001)				

†Paired t-test between SWD_{max} of the two periods

‡Paird t-test between $CSWD_{max}$ of the two periods

Both SWD_{max} and $CSWD_{max}$ showed highly significant ($P<0.001$) positive linear increases with increasing altitude during both periods. However, respective regression slopes did not differ significantly ($P<0.05$) between the two periods as their 95% confidence intervals overlapped with each other (Table 11).

Table 11. Slopes of linear regressions of monthly maximum soil water deficit (SWD_{max}) and maximum cumulative soil water deficit ($CSWD_{max}$) against altitude during the two 29-year periods in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

	1961-1989			1990-2018		
	Slope ($\times 10^{-2}$ mm month^{-1} m^{-1})	**95% CI† ($\times 10^{-2}$ mm month^{-1} m^{-1})**	**Adj.R^2**	**Slope ($\times 10^{-2}$ mm m^{-1})**	**95% CI† ($\times 10^{-2}$ mm m^{-1})**	**Adj.R^2**
SWD_{max}	1.712	1.002 - 2.422	0.769	2.001	1.283 - 2.719	0.817
$CSWD_{max}$	4.187	2.575 - 5.799	0.795	3.886	2.298 - 5.473	0.774

†95% confidence interval of the regression slope.

Dry-Season Index (DSI)

Time courses of the DSI (i.e. maximum annual CSWD of each PSP) for the two 29-year periods are shown in Fig 10. During both periods, the DSI of the higher altitude PSPs (i.e. RLG, HKG, PTG and HTN) were consistently higher than those at the lower altitudes (KDN and PTD, with the DSI of the mid-altitude plots (ENS) being intermediate. None of the time courses satisfied the Shapiro-Wilk test of normality. The Mann-Kendall statistic (τ) was significantly ($P<0.05$) positive for time courses of all PSPs during the 1961-1989 period (Table 12). In contrast, during the 1990-2018 period, the Kendall τ was significantly ($P<0.05$) negative in all PSPs except ENS where it was significant at $P<0.1$.

Fig 10. Time courses of Dry-Season Index (DSI) during 1961-1989 (A) and 1990-2018 (B) periods in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient. DSI in a given year is the maximum cumulative soil water deficit (CSWD) observed within that year.

Table 12. Mann-Kendall statistic (τ) of the time courses of dry-season index (DSI) during the two 29-year periods in the permanent sampling plots in tropical rainforests of Sri Lanka across an altitudinal gradient.

		Kendall τ			
PSP	**Altitude (m)**	**1961-1989**	**P†**	**1990-2018**	**P†**
KDN1	117	0.374	0.0061	-0.289	0.0351
KDN2	174	0.353	0.0096	-0.340	0.0159
PTD1	509	0.342	0.0120	-0.305	0.0295
PTD2	618	0.342	0.0120	-0.305	0.0295
ENS1	1042	0.388	0.0039	-0.249	0.0599
ENS2	1065	0.362	0.0069	-0.249	0.0599
RLG	1668	0.327	0.0151	-0.294	0.0264
HKG	1804	0.384	0.0034	-0.281	0.0325
PTG	2080	0.389	0.0030	-0.286	0.0296
HTN	2132	0.305	0.0200	-0.286	0.0296

†Probability of Kendall τ=0.

Discussion

Importance of the findings of this study

The range of altitudes covered in this study is broader than those covered in previous studies [8–10] and as such provides a comprehensive and complete picture of the climate and soil water availability of TRFSLs. It revealed important within-year variation patterns of key climatic variables and soil water deficits experienced by TRFSLs across the whole altitudinal range of their occurrence. Furthermore, it also quantified the variation of long-term averages of these climate and soil variables with altitude. The variation patterns identified and quantified in this work will be useful in determining how climate and soil water availability controls the species composition, structure, and primary productivity of TRFSLs when relationships are established between these ecosystem properties and environmental variations. Such relationships will enable prediction of the responses of TRFSLs to long-term climate change and provide a valid foundation for key policy decisions for protection and future sustenance of this vital ecosystem of Sri Lanka.

Key findings on climate variation and their implications

Temperatures

The observed long-term annual and monthly variations of temperature show that the rainforests in the lower altitudes experience higher temperatures which have lower diurnal and within-year fluctuations. In contrast, the TFRs in the higher altitudes experience lower temperatures which have higher diurnal and within-year fluctuations. These fluctuations, when expressed as a percentage of the prevailing temperatures, are greater at the higher altitudes.

While the observed reduction of air temperature with altitude is expected, the rate of reduction reveals important differences, which require important functional shifts in tree species present in TRFSLs at different altitudes. For example, T_{min} shows a greater sensitivity to altitude than T_{max} (Tables 5 and 7), thus indicating that lower temperatures at night decrease faster with altitude than higher temperatures during the daytime. This requires the tree species at higher altitude montane forests to have greater tolerance to lower temperatures (i.e., cold tolerance) than those at lower altitude lowland evergreen forests. On the other hand, the lower rate of decline of T_{max} indicates that adaptations to tolerate higher temperatures during the daytime may be less crucial than evolving adaptations to tolerate cold tolerance for tree species in tropical montane forests.

The differential sensitivity of T_{min} and T_{max} to altitude causes the increase of DTR with altitude (Tables 2 and 7). This means that the day-night temperature fluctuation as a percentage of the prevailing average temperature regime becomes greater with increasing altitude. This also has important implications for evolving tree species with adaptations required to achieve survival and higher productivity in TRFSLs at different altitudes. It means that tree species in tropical montane forests need adaptations to a lower temperature regime with greater fluctuations whereas tree species in tropical lowland evergreen forests require adaptations to a warmer environment with fluctuations of a lower amplitude.

In this regard, the impact of greenhouse gas-induced climate warming [4] on future T_{min} and T_{max} of TRFSLs will be crucial in specifying the adaptations that tree species of TRFSLs need to evolve in their physiology. In an analysis of long-term temperature data from Nuwara Eliya in Sri Lanka (altitude 1895 m), Sonnadara [45] found DTR to have decreased significantly with time due to an increasing trend in T_{min}, especially during the colder periods of the year, while the T_{max} remained unchanged. The decreasing trend of DTR with time in parallel to the global warming trend agrees with the altitudinal trend of DTR found in the present study (Tables 2 and 7). As the temperatures increased with decreasing altitude, DTR narrowed as the T_{min} increased faster than T_{max}. The faster decrease of T_{min} with altitude agreed with the faster increase of T_{min} with global warming, whereas the slower decrease of T_{max} with altitude contrasted with the absence of a T_{max} trend with global warming. Therefore, there is partial agreement between the temperature trends in response to decreasing altitude and those shown in response to global warming.

The present analysis reveals that within-year variations of T_{max} and T_{min} (Fig 2) cause substantial within-year fluctuation in DTR (Fig 3B). At all altitudes, DTR shows a peak during the three-month period from February to April and a trough during the period from June to August. The peak period occurs mainly because of a peak in T_{max} while the trough period occurs because of the combined effect of a trough in T_{max} and a peak in T_{min} during June to August. These within-year variations in T_{max}, T_{min} and DTR further emphasize the differing temperature regimes at lower and higher altitudes and consequent need for the rainforests to evolve different eco-physiological mechanisms for optimum adaptation to their respective environment. Accordingly, tree species at higher altitude rainforests need adaptations to survive and function at a higher day-night temperature differential which can reach as high as 11 – 12°C during March. On the other hand, tree species at lower altitudes require eco-physiological adaptations to a day-night temperature differential, which is only about 50% of the maximum DTR at higher altitudes. In a seedling experiment with ten neo-tropical tree species, Cheeseman and Winter [46] showed that the seedling response to different DTR regimes differed among pioneer and non-pioneer species, with the pioneers showing greater adaptation than non-pioneers in their growth response to non-optimum temperatures and DTRs. Accordingly, Cheeseman and Winter [46] highlighted the importance of thermal acclimation potential of key physiological processes such as photosynthesis and respiration of tropical tree species. In this regard, Cunningham and Read [47] found that the photosynthesis of temperate tree species can acclimate to a broader temperature range than tropical tree species. They attributed this difference in acclimation potential between temperate and tropical tree species to the day-night and seasonal fluctuations that the temperate species experience in their natural environment. Therefore, the different tree species that are found in TRFSLs at different altitudes probably require acclimation of their key physiological processes in accordance with the within-year and day-night temperature fluctuation at their respective altitudes. Such variation in acclimation potential could have important implications on how these forest ecosystems and their tree species respond to global warming and climate change [48,49].

Rainfall and solar irradiance

The respective analyses of this study reveal that both R_F and S_R experienced by TRFSLs decrease with increasing altitude (Tables 2 and 7). These trends should be considered specific to the altitudinal gradient covered in this study as other altitudinal gradients in tropical rainforests of other parts of the world could show different trends. As Körner [19] points out, altitudinal trends in rainfall are extremely difficult to predict because of the complex interaction of several atmospheric processes and land features that determine the moisture availability in the atmosphere to generate rainfall. In the present study, the forest plots at altitudes up to 1668 m are located on the western slope of the Central Highlands of Sri Lanka, which is on the windward side for the south-west monsoon rains, one of the two major rainy seasons experienced by TRFSLs. On the other hand, the three plots at the highest altitudes (i.e., Hakgala, Pidurutalagala and Horton Plains) are located along the eastern slope, which is on the leeward side for the south-west monsoon rains. Therefore, it is likely that the 'rain shadow effect' on the leeward side contributed to the relatively lower R_F experienced at the three highest altitude plots. The distribution of the first inter-monsoon rainfall season during the period from March to April increases towards the south-western part of the country [50]. During this period, rainfall has shown increases in all PSPs creating a minor peak in HKG, PTG and HTN. But the increase of rainfall at lower and mid altitudes was not sufficient to create a prominent peak nor a minor peak during the first inter-monsoon. During the second inter-monsoon rainfall season from October to November, even distribution of rainfall occurs throughout the country with a higher rainfall at south-western slopes. In agreement with this trend, a prominent peak was observed during the period from October to November in all PSPs, which increased with decreasing altitude. Although the north-east monsoon rains from December to

February were expected to bring higher rainfall to the eastern slopes of the Central Highlands [50], no prominent nor minor peak occurred in HKG, PTG and HTN. The greater effect of the north-east monsoon on higher altitudes compared to lower and mid altitudes probably altered the clear decreasing pattern of monthly rainfall along the altitudinal gradient in December and January. However, the within-year variation R_F at different altitudes shows that the three highest altitudes have consistently lower R_F throughout the year than the lower and mid-altitude plots (Fig 4). Therefore, atmospheric phenomena and land surface features other than their location on the Central Highlands probably play a role in determining the altitudinal variation of R_F across TRFSLs. The observation that both annual total R_F and monthly R_F of the mid- (Sinharaja-Enasalwatte, ENS1 and ENS2) and higher-mid (Rilagala, RLG) altitudes are at intermediate levels between those of the lowest and highest altitudes indicates that the rainfall variation across this altitudinal gradient is at least partially linked to factors and phenomena that vary with altitude.

Even though the intensity of incident solar radiation under clear skies increases with increasing altitude because of increased atmospheric transmissivity at higher altitudes [19], variations in cloudiness and atmospheric moisture (i.e., fog, mist) determine the actual S_R experienced by vegetation. It is possible that greater cloudiness, fog, and mist contributed to the decrease of S_R experienced by TRFSLs at higher altitudes. It is notable that the inverse relationship between R_F and S_R that is observed across the different climatic zones of Sri Lanka does not apply to the altitude range occupied by the TRFSLs [51]. However, the two peaks of monthly S_R observed at all altitudes in February – April and August – September periods (Fig 5) partially coincide with two periods of relatively lower R_F (Fig 4). In addition, they also correspond to the two periods during which the Earth's orbit around the sun brings it directly above Sri Lanka. Hence, it is likely that the two above phenomena combined to determine the within-year variation pattern of S_R observed across the TRFSLs of the present study.

Soil water deficits

Computation of the soil water deficits, both on a separate monthly basis (SWD) and on a cumulative basis (CSWD), across the range of altitudes traversed by the TRFSLs (Fig 6) is an important contribution of this study to the existing knowledge base. As acknowledged by Malhi and Wright [38], SWD and CSWD calculated using their method, provides a relative measure of the dry season length and intensity. The computation of SWD and CSWD uses monthly evapotranspiration rates (Et) derived from equation 2 with the coefficients obtained from Malhi and Wright [38]. Even though these coefficients were derived from measurements in South American TRFs in the Amazonia, the Et values reported from published literature on TRFs in Asia, South America and Africa (Table S1) confirmed the validity of the coefficients used. The Table S1 also includes a compilation of Et measurements from 138 tropical forests [52]. All measured or estimated monthly Et values were within a narrow range between 97 and 125 mm month^{-1}. The monthly Et values in the Asian region with annual rainfalls that are comparable to those of the present study are within an even narrower range between 109 and 125 mm month^{-1}. The TRFs in the Congo basin where the monthly Et values are lower (97 – 99 mm month^{-1}) have a lower annual rainfall regime than the sites of the present study. The TRFs in the Amazonia are intermediate between those in Asia and the Congo basin while having a rainfall regime which is comparable to that of the present study. The value of 118 mm month^{-1} used as Et_o in equation 2 represents the Et of a TRF which is not experiencing a water deficit. This is within the range of Et values reported for TRFs in Asia. The value of -0.3625 mm (Et month^{-1}) mm^{-1} (Soil water deficit, SWD) is a measure of the sensitivity of Et to SWD. The maximum monthly SWD observed in the present study was 54 mm (at Pidurutalagala where the annual rainfall was 1926 mm y^{-1}), which would reduce Et_o from 118 mm $month^{-1}$ by 20 mm $month^{-1}$. The resulting Et at Pidurutalagala would be 98 mm $month^{-1}$ which is similar to the Et values reported for the lower rainfall regimes in the Amazonia and in the Congo basin. As such, values of the two coefficients of equation 2 have a strong validation from Et values reported in literature from all three continents which contain substantial areas of tropical rainforests.

Computed SWD values showed that TRFSLs at all altitudes experienced a dry season from February to March, which coincides with the lower rainfall that prevails during this period. The lower rainfall levels at the three highest altitudes caused their higher SWDs. On the other hand, the relatively higher rainfall levels, especially during March were responsible for the lower SWDs at the lowest altitudes. It is notable that CSWD increased continuously over the three-month period from January to March at the three highest altitudes while CSWD increased only up to February at mid- and lower altitudes. Furthermore, the three highest altitudes experienced a second, smaller peak of SWDs in June and a 2 to 3-month period of continuous increase of CSWD from May to July. In contrast, the mid- and lower altitudes did not experience this second peak of SWD and CSWD.

The Dry-Season Index (DSI), which was the maximum CSWD observed in a given year in each PSP gives a relative measure of the intensity and duration of the ‘dry’ season [38] during which the forests are likely to experience water stress. Results of this study showed that DSI increases with increasing altitude so that the montane forests at higher altitudes are more likely to experience droughts of greater intensity and duration than the lowland rainforests at lower altitudes.

The above variations in SWD and CSWD, when considered in conjunction with the corresponding monthly variations of temperature (Figs 2 and 3) and rainfall (Fig 4) means that the montane forests at the higher altitudes experience greater seasonality in terms of both soil water availability and temperature. Accordingly, the tree species in the montane forests need to evolve physiological mechanisms to adapt to this seasonality of climate and soil water availability [53–55]. In contrast, tree species in the lowland evergreen forests do not have a critical need to evolve such adaptations to climate seasonality.

Variability of climate and soil water deficits and its implications

In addition to the long-term averages and within-year variations of key climatic variables and soil water deficits experienced by TRFSLs, the present study also quantified the inter-annual variability in the climate and soil water availability that are experienced by this ecosystem at different altitudes. These assessments of climate and soil variability could provide indicators on the dynamics and successional trajectories of TRFSLs as long-term environmental variability influences the functional properties of plant species that thrive in these lowland evergreen and montane forest ecosystems [56–59].

A key finding of the assessment of inter-annual variability of climatic variables, quantified in terms of their CV (Figs 7 and 8) was the substantially higher variability in rainfall and soil water deficits in comparison to the variability of the four temperature variables. This agrees with the findings of

De Costa [5] in a long-term analysis of temperature and rainfall data at a series of locations representing different agroclimatic zones of Sri Lanka. The higher variability of rainfall can be attributed to the complex interaction of atmospheric processes and mechanisms responsible for rainfall generation and their interaction with altitude and land surface properties. Furthermore, atmospheric phenomena such as the El-Niño Southern Oscillation (ENSO) [11,56,58,60] and Indian Ocean Dipole [61,62] probably contribute to the greater inter-annual variability of rainfall. It is notable that the magnitude of variability of rainfall shows little within-year variation (Fig 8A). In contrast, magnitudes of variability of the temperature variables showed appreciable within-year variation (Fig 7). The substantially higher inter-annual variability of SWD and CSWD, when taken in conjunction with the higher variability of rainfall, shows that despite being in a relatively high-rainfall environment, tree species in TRFSLs may require adaptations and mechanisms to buffer them against these substantial fluctuations in water availability.

Comparison of long-term climate of tropical rainforests of Sri Lanka (TRFSLs) with the climate of tropical rainforests in other parts of the world

The ranges of climatic variables (i.e. T_{max}, T_{min}, R_F and S_R) observed in the present study broadly agreed with the ranges reported for tropical rainforests elsewhere [38,63–67] because all these forests are located within the same range of latitudes. Similarly, the range of maximum cumulative soil water deficit ($CSWD_{max}$) observed in the TRFSLs of this study (Tables 4 and 10) was within the corresponding range of Malhi and Wright [38] who termed $CSWD_{max}$ as the dry season index (DSI).

However, the altitudinal trends of climatic variables observed in the present study showed only partial agreement with the altitudinal trends observed in other studies [68,69]. The reductions of annual means of T_{max} and T_{min} with increasing altitude observed in the present study agreed with the trends observed in other studies. However, the decreasing trends of annual R_F and daily mean S_R of this study were different from the corresponding patterns reported in other work. For example, Dieleman et al. [69] observed annual total R_F increasing with increasing altitude. On the other hand, Wallace and McJannet [68] observed a reduction of annual total R_F from the low (i.e. 30 m) to the mid (1050 m) altitude, which was followed by a substantial increase at the high (1560 m) altitude. Similarly, in contrast to the continuous decrease of daily mean S_R of the present study, Wallace and McJannet [68] reported an increase from low to mid altitude, followed by a substantial decrease at the high altitude.

The increasing temporal trends of T_{max} and T_{min} observed in the present study (Table 8) agreed with similar warming trends in other tropical rainforests elsewhere [38,64,67]. However, the rates of increases of T_{max} and T_{min} (0.13 – 0.23^{o}C per decade) were lower than the mean rate of 0.26^{o}C per decade observed by Malhi and Wright [38] for the rainforests in all tropical regions of the world (i.e. South America, Asia and Africa). However, except for the rates of increase of T_{max} during 1990-2018, the rates of increases of both T_{max} and T_{min} in the present study were greater than the rate of 0.15^{o}C per decade reported for rainforests in North Queensland, Australia by Bauman et al. [67] for the 1971-2019 period.

The temporal decline of annual total R_F observed for the 1961-1999 period is in agreement with the moderate decreasing trend observed for the Asian region by Malhi and Wright [38]. Similarly, Asefi-Najafabady and Saatchi [70] and Zhou et al. [71] observed strong decreasing trends in R_F in the rainforests of West and Central Africa and Congo during the first decade of the 21st century. However, Malhi and Wright [38] also reported that many tropical regions did not show a significant trend in R_F. This is similar to the absence of a R_F trend that was observed in the present study during the 1990-2018 period. The higher variability of R_F in comparison to the lower variability of T_{max} and T_{min} in the present study agrees with a similar observation in Malhi and Wright [38]. On the other hand, Gloor et al. [66] observed an increasing trend in annual total R_F in the humid tropical regions of the Amazon since 1990. Gloor et al. [66] further observed an increasing trend in the wet-season R_F while observing a decreasing trend in the dry-season R_F.

It is notable that both monthly SWD_{max} and $CSWD_{max}$ had decreased from the 1961-1989 period to the 1990-2018 (Table 10). The observation that the intensity and duration of the dry-season (as quantified by the DSI) decreased during the 1990-2018 period (Fig 9 and Table 12) supports the above decreases of SWD_{max} and $CSWD_{max}$. This is primarily because of the decreasing trend in R_F during 1961-1989 and the absence of a trend during 1990-2018. This contrasts with the increasing trend in $CSWD_{max}$ that was observed by Malhi and Wright [38] for rainforests in South-West India during the 1970-1998 period. Asefi-Najafabady and Saatchi [70] also observed a continuing drying trend in the TRFs of West and Central Africa from the 1970s onwards. However, similar to the decrease of $CSWD_{max}$ in the present study, Malhi and Wright [38] also observed decreasing trends in TRFs of several tropical sub-regions of the world including Eastern Malaysia, Southern

Congo, Central America and North-East Amazonia. On the other hand, Bauman et al. [67] did not observe a temporal trend of $CSWD_{max}$ in TRFs of North Queensland from 1971 to 2019.

Supporting information

S1 Table. Evapotranspiration (Et) values of tropical rainforests in different continents as reported in literature.

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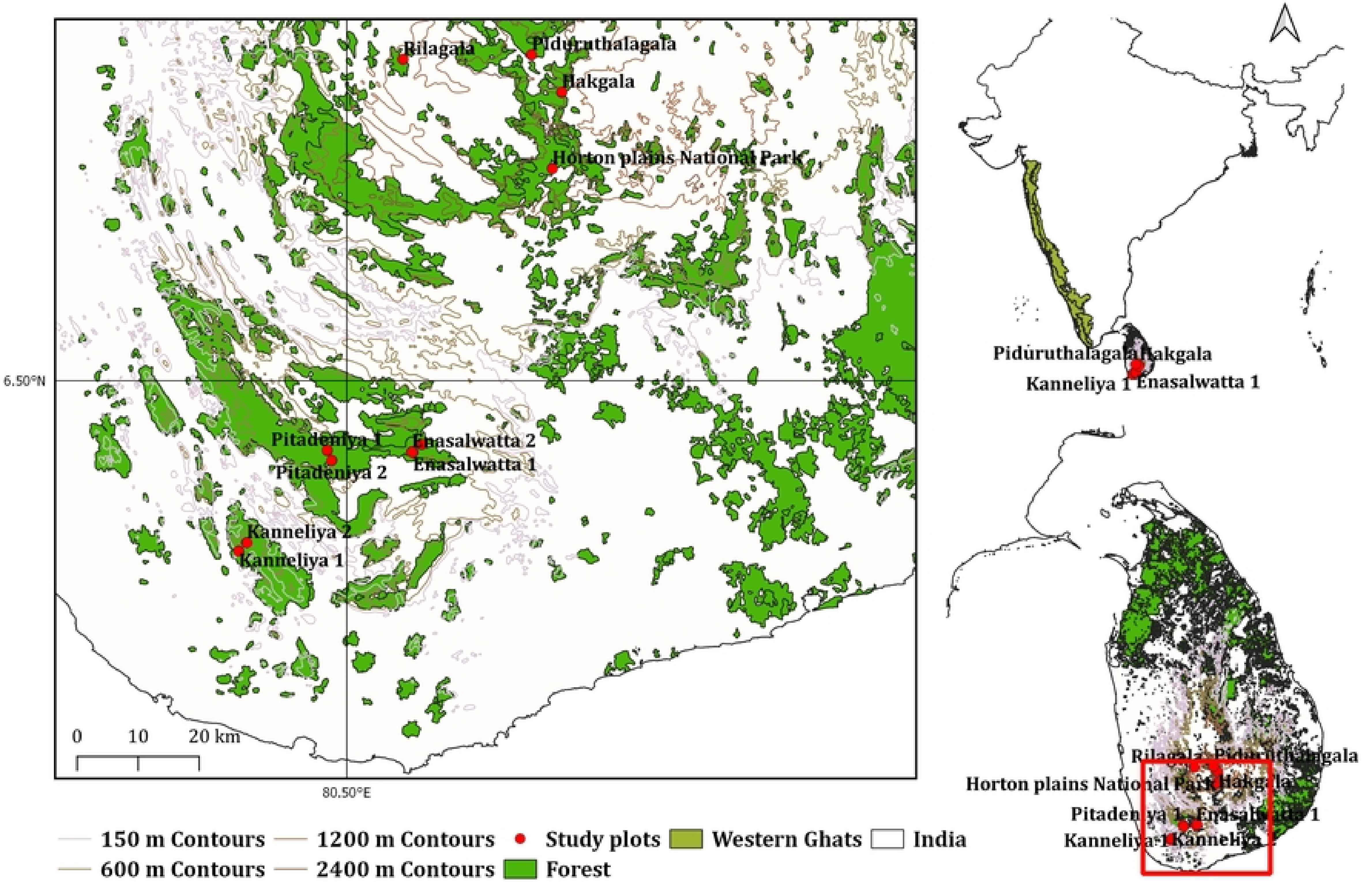

Rilagala
Piduruthalagala
Hakgala
Horton plains National Park
Pitadeniya 1
Pitadeniya 2
Enasalwatta 2
Enasalwatta 1
Kanneliya 2
Kanneliya 1
6.50°N
80.50°E
0 10 20 km
150 m Contours
600 m Contours
1200 m Contours
2400 m Contours
Study plots
Forest
Western Ghats
India

Fig 1

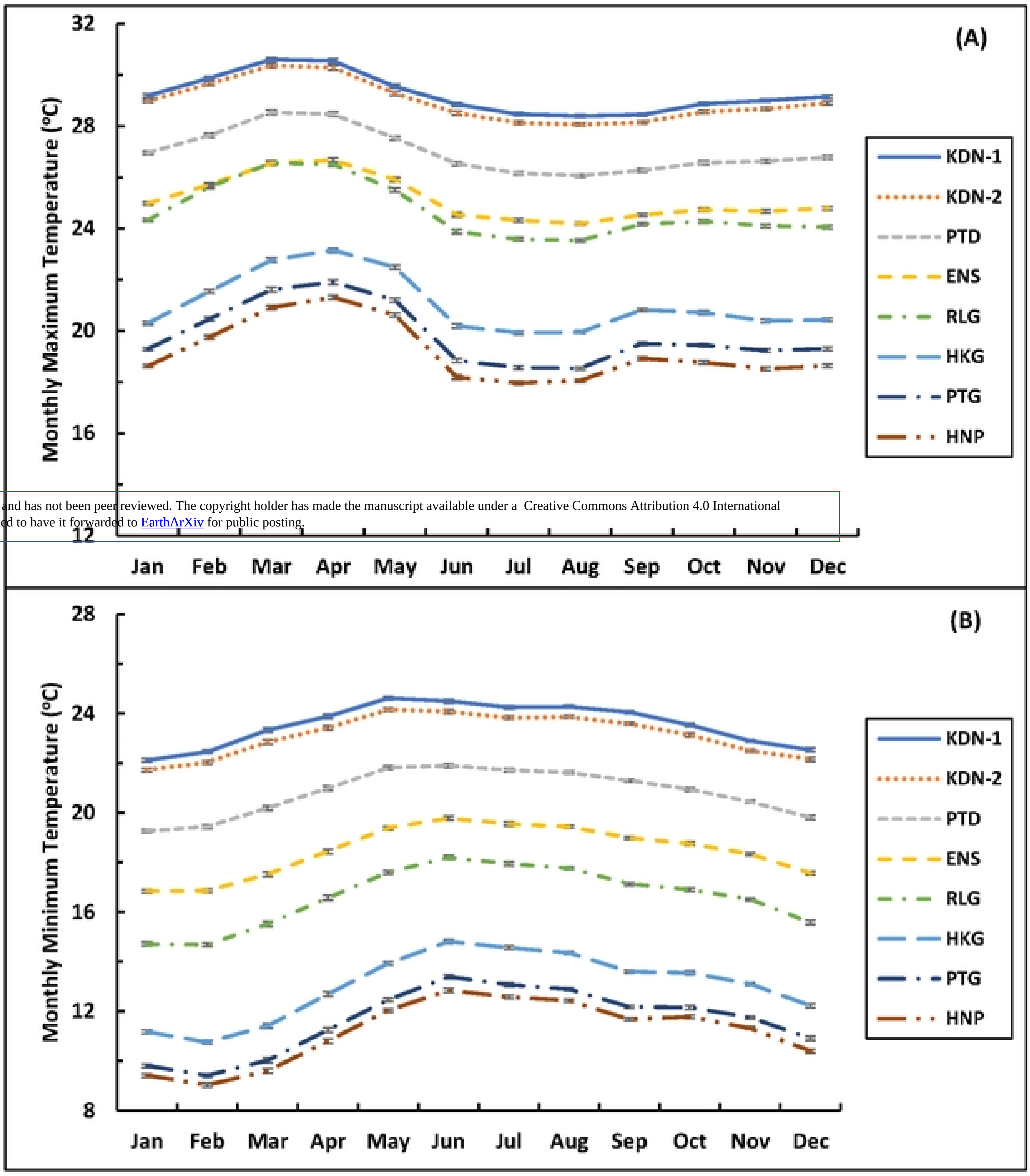
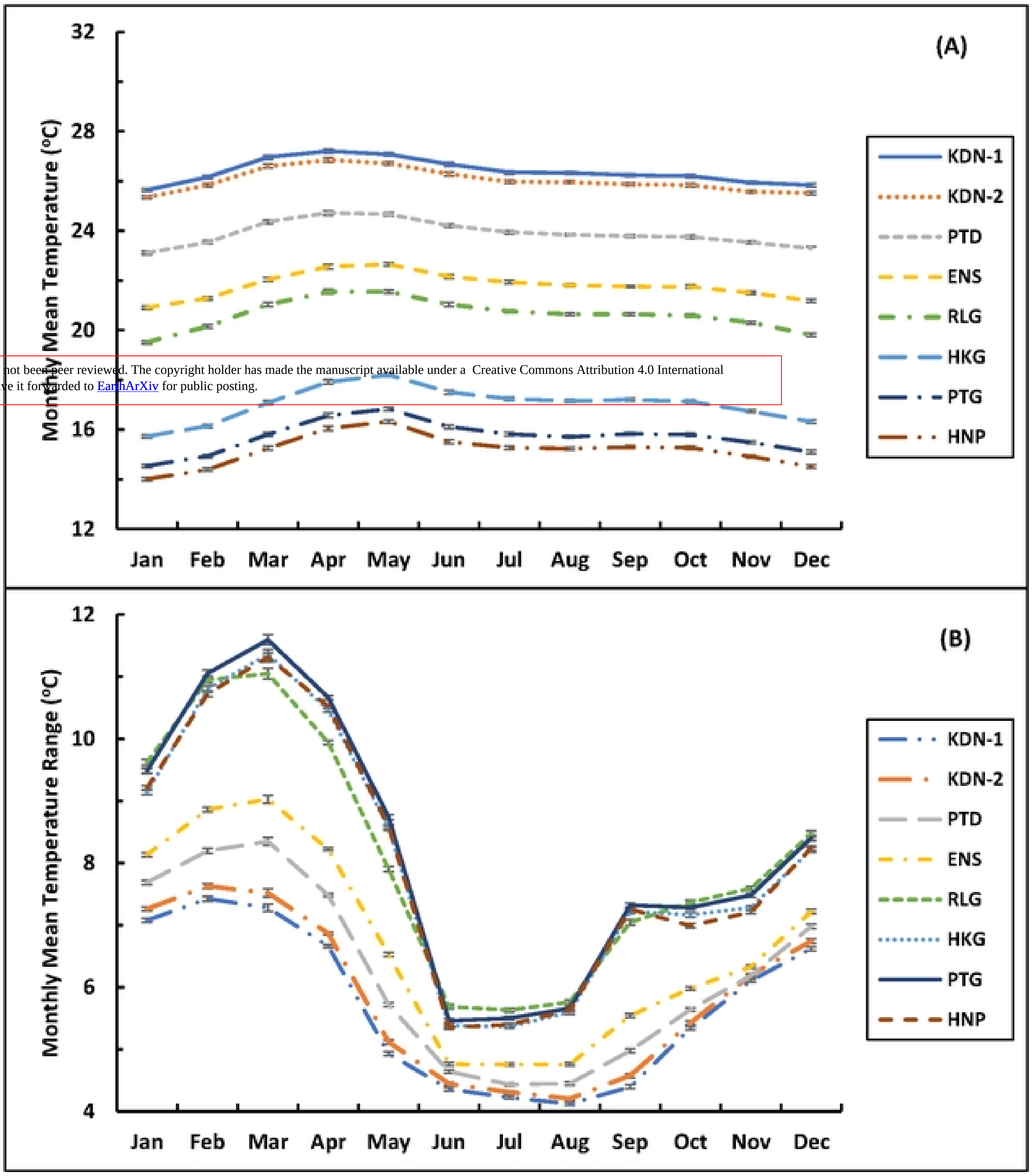
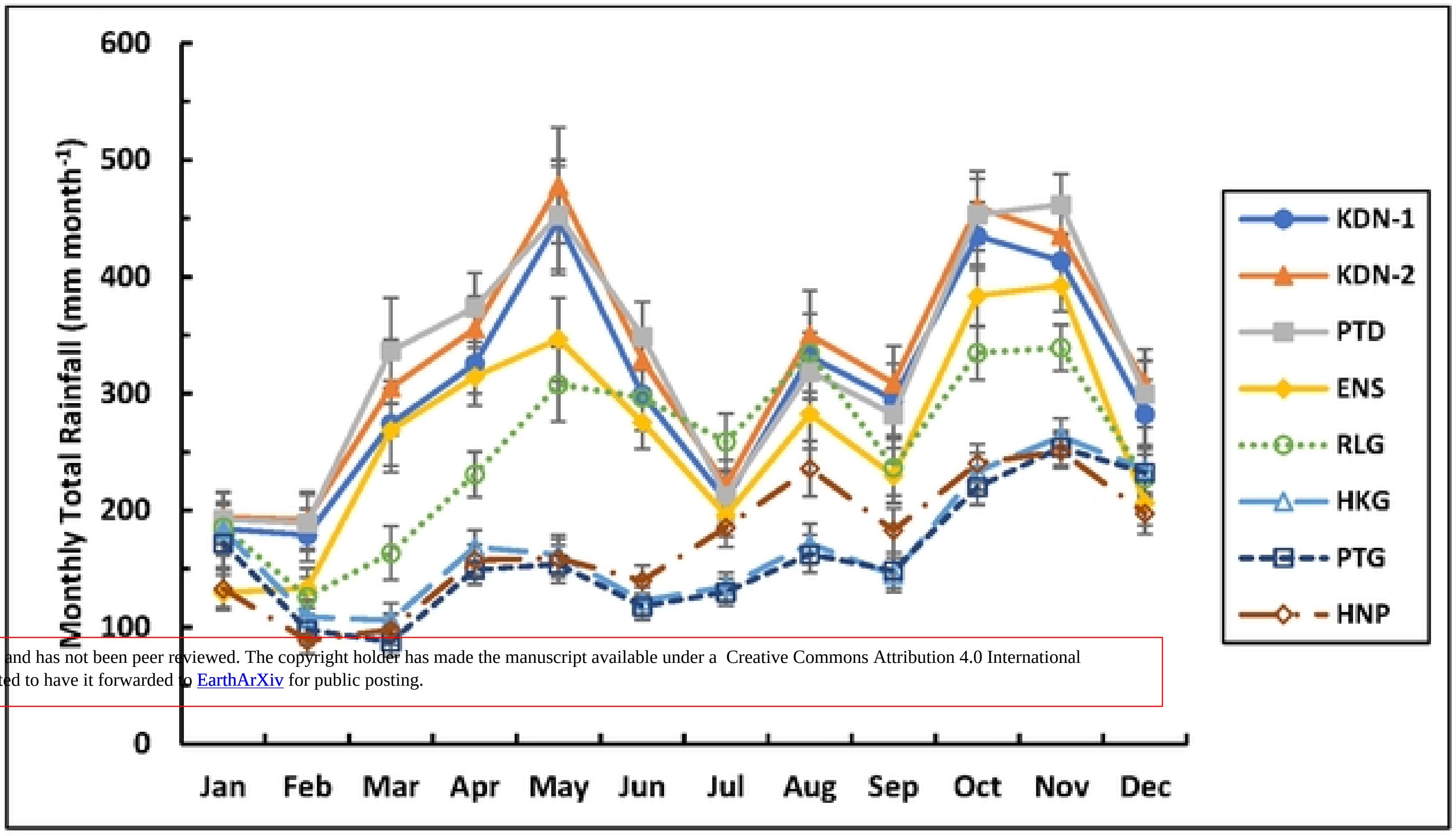

(A)
Monthly Maximum Temperature (°C)
32
28
24
20
16
12
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP
(B)
Monthly Minimum Temperature (°C)
28
24
20
16
12
8

Fig 2



(A)
Monthly Mean Temperature (ºC)
32
28
24
20
16
12
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP
(B)
Monthly Mean Temperature Range (ºC)
12
10
8
6
4
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP

Fig 3



600
500
400
300
200
100
0
Monthly Total Rainfall (mm month-1)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP

Fig 4

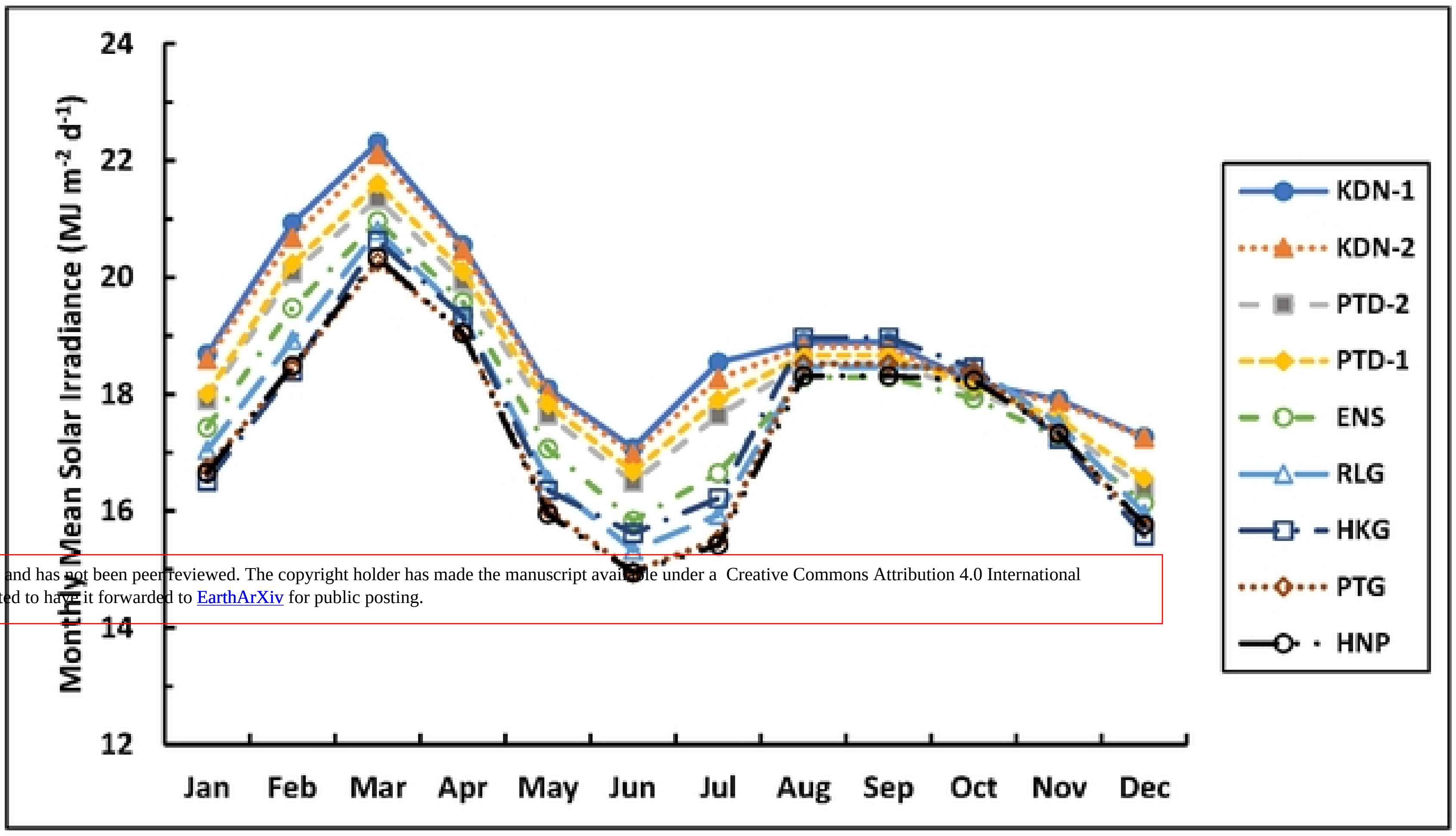

Monthly Mean Solar Irradiance (MJ m-2 d-1)
24
22
20
18
16
14
12
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
KDN-1
KDN-2
PTD-2
PTD-1
ENS
RLG
HKG
PTG
HNP

Fig 5

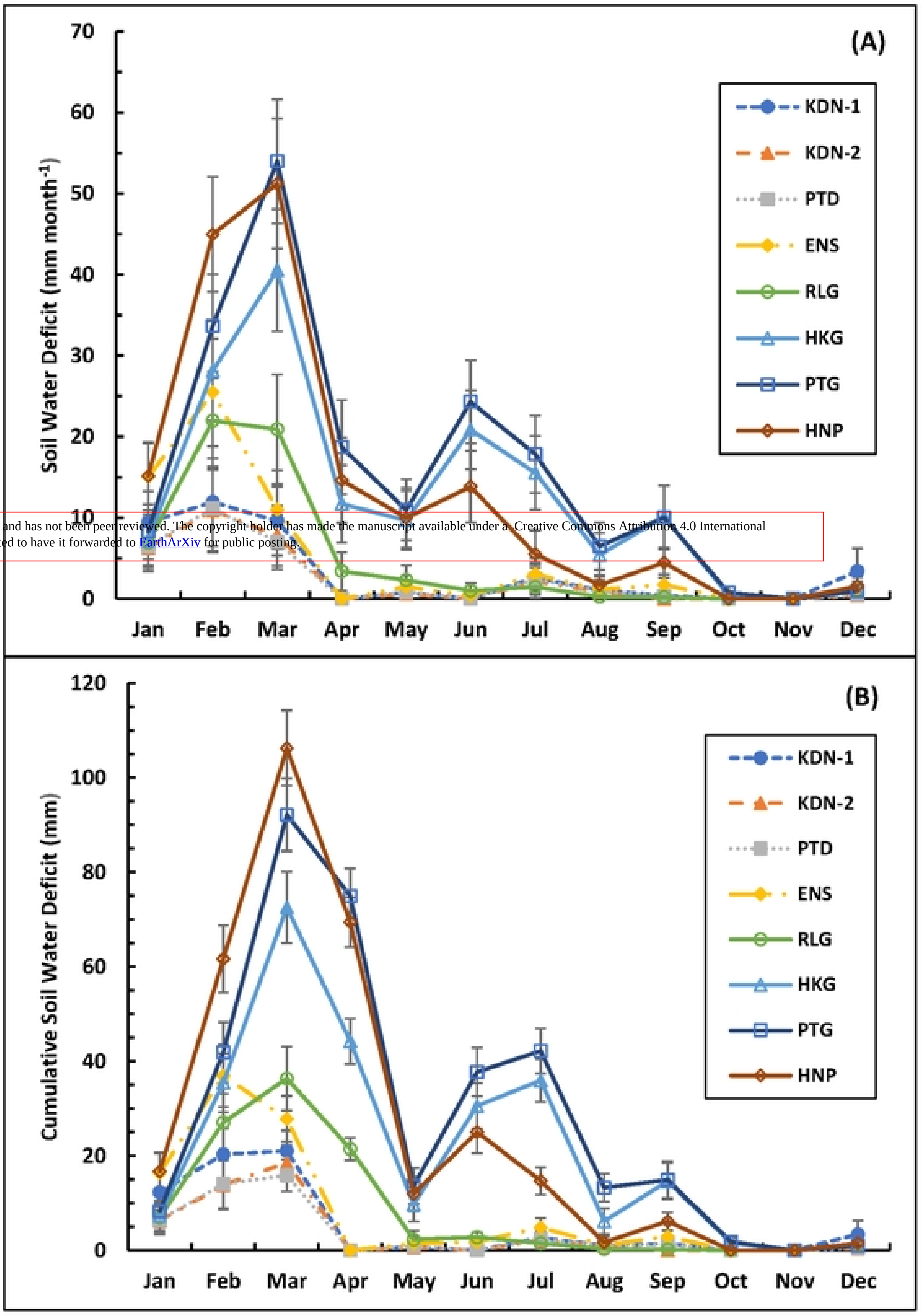
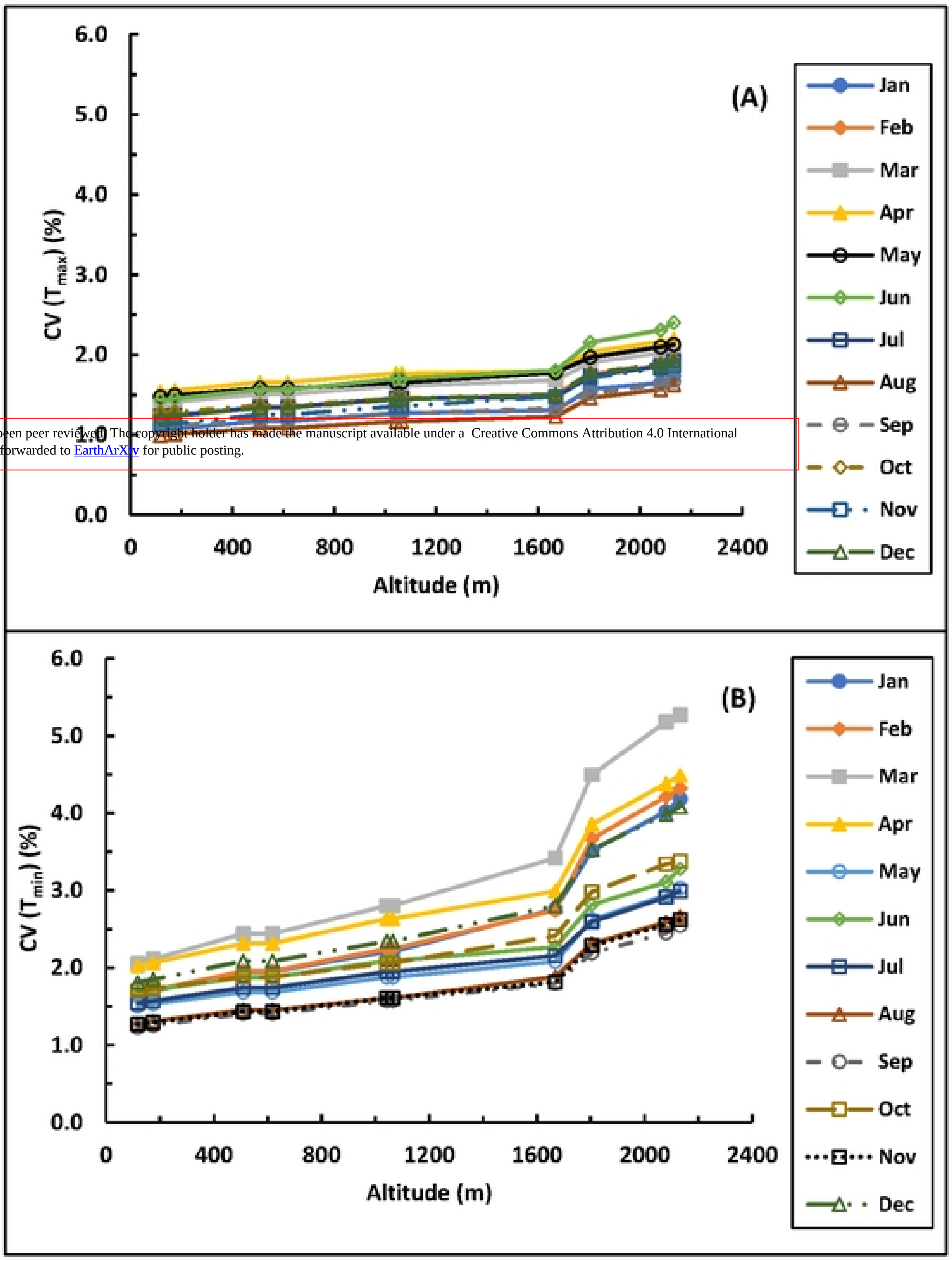

(A)
Soil Water Deficit (mm month-1)
0
10
20
30
40
50
60
70
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP
(B)
Cumulative Soil Water Deficit (mm)
0
20
40
60
80
100
120
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
KDN-1
KDN-2
PTD
ENS
RLG
HKG
PTG
HNP

Fig 6



(A)
CV (T_{max}) (%)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
(B)
CV (T_{min}) (%)

Fig 7

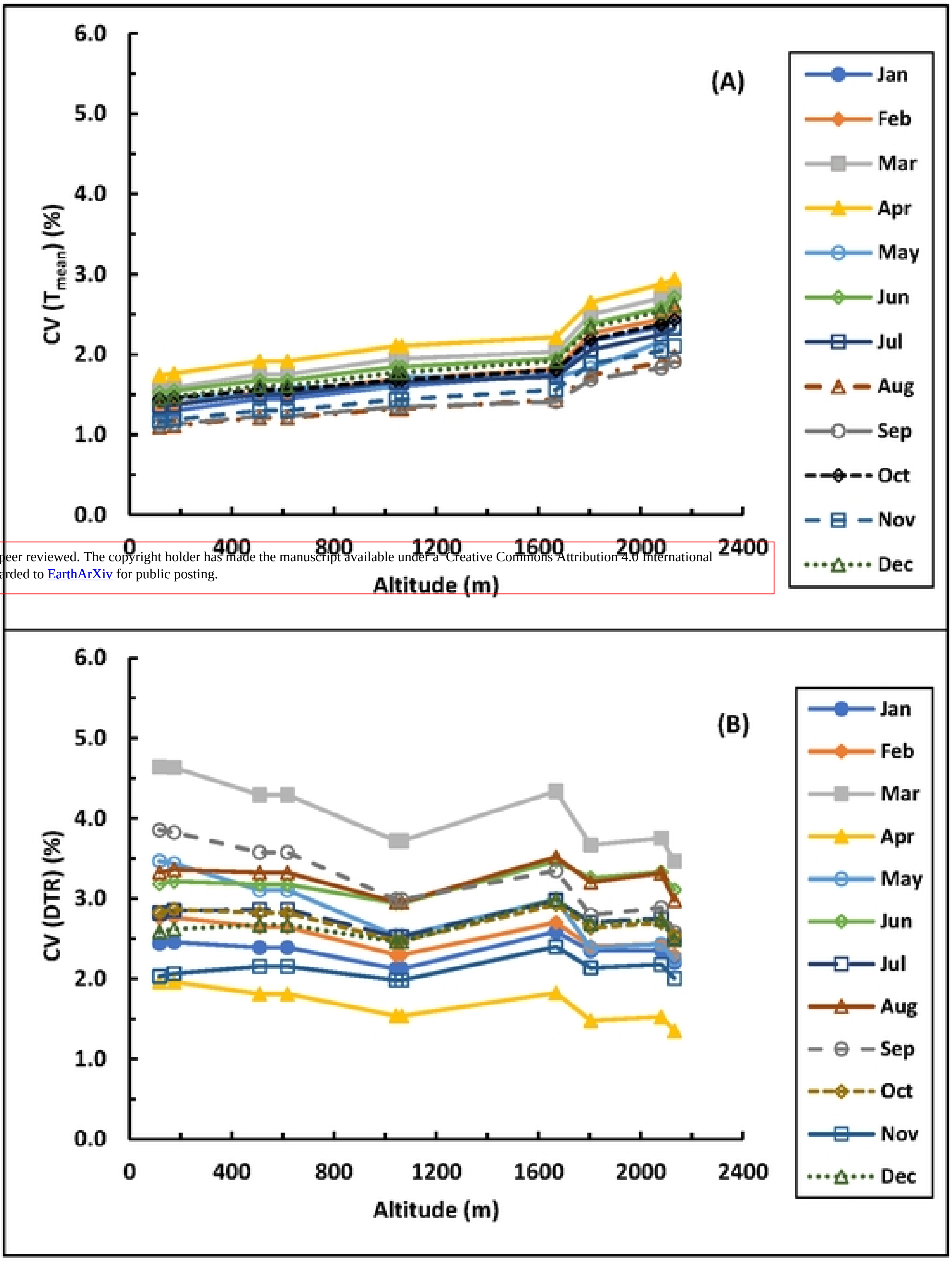

(A)
CV (T_mean) (%)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
(B)
CV (DTR) (%)
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig 8

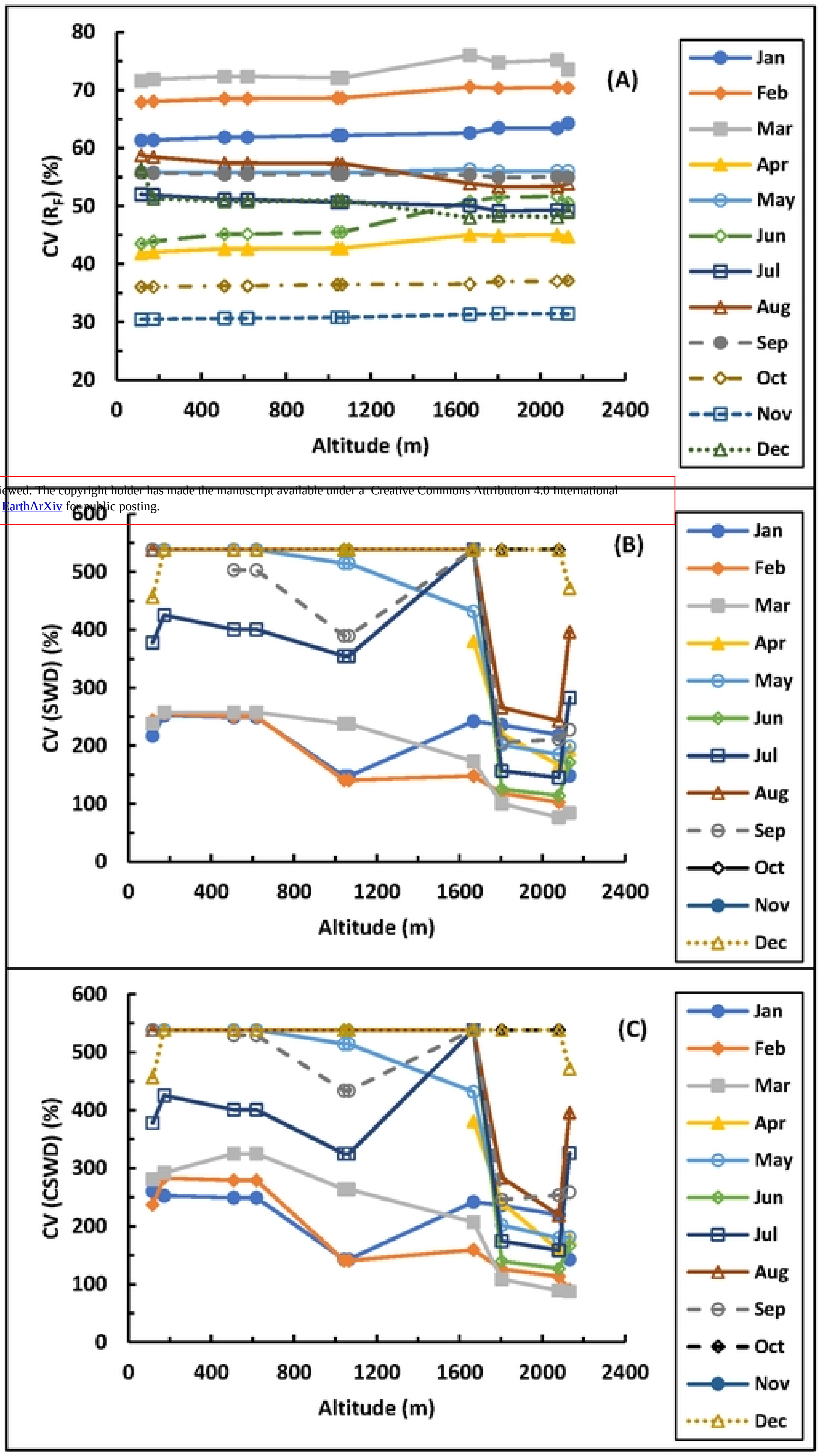

(A)
CV (R_F) (%)
80
70
60
50
40
30
20
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
(B)
CV (SWD) (%)
600
500
400
300
200
100
0
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
(C)
CV (CSWD) (%)
600
500
400
300
200
100
0
0
400
800
1200
1600
2000
2400
Altitude (m)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Fig 9

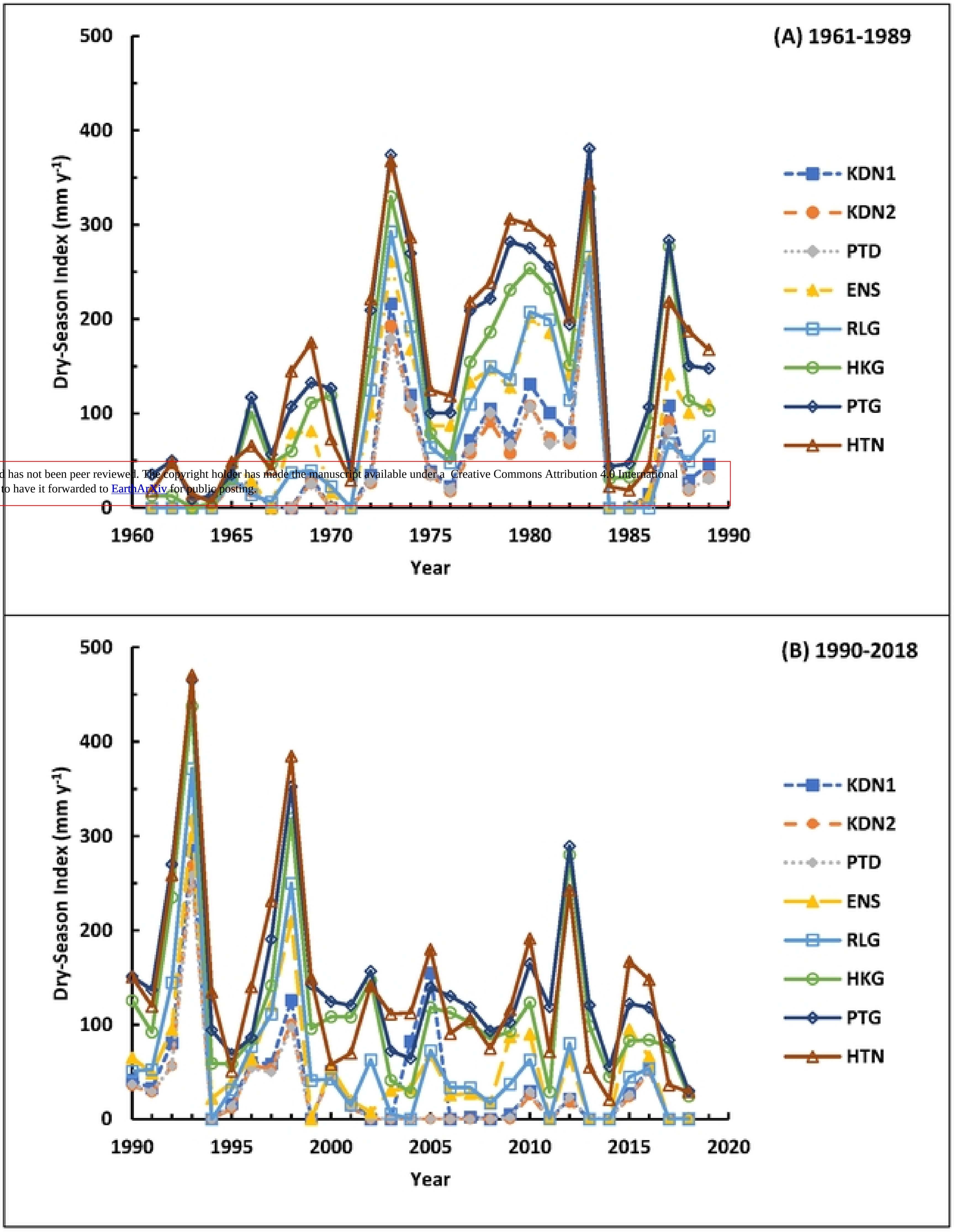

(A) 1961-1989
Dry-Season Index (mm y-1)
500
400
300
200
100
0
1960
1965
1970
1975
1980
1985
1990
Year
KDN1
KDN2
PTD
ENS
RLG
HKG
PTG
HTN
(B) 1990-2018
Dry-Season Index (mm y-1)
500
400
300
200
100
0
1990
1995
2000
2005
2010
2015
2020
Year
KDN1
KDN2
PTD
ENS
RLG
HKG
PTG
HTN

Fig 10