Variation of floristic diversity, community composition, endemism, and conservation status of tree species in tropical rainforests of Sri Lanka across a wide altitudinal gradient

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Abstract

Tropical rainforests in Sri Lanka are considered as biodiversity hotspots. However, their existence is threatened by multiple climatic and anthropogenic drivers. Our objective was to assess the diversity, endemism and conservation status of these rainforests across a wide altitudinal range. We conducted a complete census of all trees having $\geq$ 10 cm diameter at breast height in ten one-hectare permanent sampling plots of tropical rainforests from 100 to 2200 m above mean sea level and determined altitudinal trends in tree diversity, floristic composition, endemism and conservation status of tree taxa. While community-scale tree diversity decreased with increasing altitude, substantial altitudinal differentiation of tree taxa was observed. Increasing day-night temperature difference (DTR), decreasing rainfall and increasing cumulative maximum soil water deficit ($CSWD_{max}$) with increasing altitude decreased tree diversity and the percentage of endemic species while increasing the percentage of endangered species. These trends show that the ability to colonize the higher altitudes, where lower temperatures and higher soil water deficits act as climate constraints, is a major determinant of tree diversity and endemism in Sri Lankan rainforests across altitude gradients. This hypothesis is supported by the observed increases of the percentages of endangered and vulnerable species from mid- to high altitudes. Most of the dominant species at different altitudes were endemic and are endangered or vulnerable. We conclude that the decrease in diversity and endemism is most likely driven by cold- and drought-sensitivity of these predominantly tropical-adapted tree species so that conservation efforts are most needed at altitudes above 1000 m.

Introduction

Tropical forests are the one of the most diverse terrestrial ecosystems on earth (Myers et al. 2000; Groombridge and Jenkins 2002) Sustenance of biodiversity of tropical rainforests is threatened by several natural and anthropogenic processes (Malhi et al. 2014). Atmospheric warming, increased frequency of droughts and forest fires caused by climate change have brought many plant species out of their favourable ecological range (Esquivel-Muelbert et al. 2019; Sullivan et al. 2020). Human activities such as deforestation and over-exploitation have caused habitat loss for many flora and fauna in forest ecosystems (Lewis et al. 2015). Accordingly, the need for assessment of conservation needs at the ecosystem and taxon level is important and urgent (Edwards et al. 2019).

Altitudinal gradients provide an excellent natural setting for investigating ecosystem responses to long-term environmental change, which would otherwise necessitate long-term observation (Malhi et al. 2010; Clark et al. 2015). The composition and diversity of an ecosystem at a given altitude represents the functional balance of long-term evolutionary processes that determine recruitment, growth, reproduction and mortality of different taxa as shaped by the climate and soil at that altitude. As climatic and soil factors vary along altitudinal gradients, variation of ecosystem composition and diversity along them shows the influence of long-term evolutionary responses to environmental change. Individual taxa differ in the range of climatic and soil factors within which their growth and reproductive performance is maximum. Accordingly, the altitudinal range across which a given taxon is present shows its favourable ecological range, which is also an indication of a taxon's resilience or vulnerability to environmental change, both gradual (e.g. climate change) and abrupt (e.g. deforestation, fire). The conservation status of a given species is a collective assessment based on its current population, ecological range and its probability of survival. Accordingly, the natural and anthropogenic changes in the environment and habitat which are superimposed on the environmental gradients along altitudes have a substantial influence on the conservation status of a given species within an ecosystem. Tropical rainforests are a primary focus in conservation initiatives as they represent an ecosystem of high biodiversity threatened by natural and anthropogenic drivers. Therefore, in the present work, we focused on assessing the conservation status of woody plant taxa in the tropical rainforests of Sri Lanka, which in combination with forests in the Western Ghats of India, had been included in the 18 originally-designated biodiversity hotspots (Myers et al. 2000). The rainforests of Sri Lanka span an altitudinal range from 100 m to 2200 m above mean sea level (asl) and include lowland wet-evergreen, lower-montane and montane forests (Gunatilleke et al. 2008). During the last three centuries, the rainforests in the South Asian Region have become

increasingly threatened with deforestation and fragmentation (Gunatilleke and Gunatilleke 1991; Reddy et al. 2016). Therefore, an assessment of the conservation status of their taxa along an altitudinal gradient provides a foundation for conservation efforts in a future changing climate.

Globally, there have been several studies of the variation of tropical rainforests along altitudinal gradients (Gentry 1988; Lieberman et al. 1996; Aiba and Kitayama 1999; Homeier et al. 2010; Clark et al. 2015; Cirimwami et al. 2019). A majority of these have focused on the variation of forest structure and biomass with only a minority focusing on the variation of floristic composition and even less on endemism and conservation importance. Tropical rainforests of Sri Lanka and those of the Western Ghats share a common tectonic plate known as the Deccan Plate, of southern Gondwana origin and their floristics is considered to be distinct from that of rainforests in the rest of tropical Asia (Ashton and Gunatilleke 1987). Therefore, our primary objective in this work was to assess the species diversity, vulnerability and conservation importance of the diverse tree communities of these tropical rainforests across their whole altitudinal range. We then aimed to identify the climatic variables that controlled tree diversity, endemism and conservation status across the altitudinal range and quantify their influence via a multiple regression approach. We carried out the above assessment by determining the (a) community-scale tree diversity; and (b) floristic composition of the tree communities in terms of endemism, conservation status, dominance and relative importance at family, genus and species levels along an altitudinal gradient. As several climatic factors related to long-term climate change vary systematically (e.g. air temperature) and non-systematically (e.g. precipitation) with altitude (Körner 2007), the above variations of the tree communities could provide indications of the vulnerability of tropical rainforests of Sri Lanka and South Asia to climate change.

In accordance with the above, we tested the following hypotheses on the altitudinal variation of tree diversity and forest structure in tropical rainforests in Sri Lanka: (1) Different tree taxa (i.e., species, genera and families) have evolved and adapted to the specific environmental conditions that prevail at a given altitude (or a narrow altitudinal range), thus leading to substantial altitudinal differentiation of tree community composition; (2) A majority of tree taxa in this humid tropical environment has evolved and adapted to a warmer temperature regime with limited diurnal fluctuation, thus leading to greater taxonomic diversity at the higher temperatures that prevail at lower altitudes and decreasing taxonomic diversity with increasing altitude; (3) Tree taxa differ in terms of their ecological range so that a limited number of taxa which occur across a broader altitudinal range than the rest can be identified; (4) Overlapping of the ecological ranges of warm-adapted and cold-adapted taxa gives rise to a mid-altitude peak in tree diversity; (5) Because of long-term evolutionary adaptation of tree species to their specific altitudes, conservation efforts against natural and anthropogenic threats are equally important across the whole range of altitudes.

Methods

Study sites and field work

We conducted this work in ten 1 ha (100 m × 100 m) permanent sampling plots (PSPs) in tropical lowland and montane rainforests in Southwestern and Central Sri Lanka. The PSPs were established along an altitudinal gradient from 117 m to 2132 m above sea level (asl) (Fig. 1) in the Kanneliya Forest Reserve (KDN1 and KDN2), Pitadeniya (PTD1 and PTD2) and Enasalwatte (ENS1 and ENS2) in the Sinharaja Man and Biosphere Reserve, Rilagala Forest Reserve (RLG), Hakgala Strict Nature Reserve (HKG), Piduruthalagala Forest Reserve (PTG) and Horton Plains National Park (HNP). At present, all these forests are strictly protected by statute. However, the Kanneliya Forest Reserve had been subjected to selective logging from mid-1960s to late-1970s. Geographic details of the PSPs are given Supplementary Table S1. Detailed analyses of the variation of climate and soil in the PSPs are reported in companion manuscripts that are under review (Madhumali et al. 2022; Sanjeewani et al. 2022).

We enumerated the PSPs from January 2019 to December 2019. All plants with woody stems with a diameter at breast height (DBH) (Height = 1.3 m) ≥ 10 cm were measured and tagged. The standardized census protocols (http://www.rainfor.org/en/manuals) used by Phillips et al. (1998) and Baker et al. (2004) were followed when measuring the DBH of trees. Taxonomic identification was done using standard keys and the reference collection at the National Herbarium of Sri Lanka at Royal Botanical Gardens, Peradeniya. Conservation status and endemism of plant species were determined using the National Red List 2012 (MOE 2012; IUCN 2020). Here, species conservation status is divided into nine categories as Extinct (EX), Extinct in The Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD) and Not Evaluated (NE). In the National Red List in Sri Lanka, an additional tag, but not an extra category, as Critically Endangered 'Possibly Extinct' CR (PE) (Online Resource 1).

Computation of vegetation indices and classification of conservation status

The overall dominance of taxa was quantified by the Importance Value Index (IVI) (Curtis and McIntosh 1951) calculated as the sum of relative density (occurrence of a taxon relative to total occurrence of all taxa), relative frequency (number of individuals of a taxon relative to the total individuals of all taxa), and relative dominance (total basal area of a taxon relative to the total basal area of all taxa). Shannon-Wiener (H') and Simpson's (D1) diversity and evenness indices and species richness (R) were calculated according to (Magurran 2013). Percentages of endemic, native and exotic species in each PSP were calculated separately based on the numbers of species and individuals. Species belonging to conservation categories CR (PE), CR and EN were pooled and designated as 'endangered (≥ END)', which along with species classified as VU, required the most urgent and highest effort in conservation. Species classified as NT and LC were also pooled as 'NT + LC' and considered as requiring the least conservation effort.

Characterization of the climatic variation across the altitudinal gradient

Long-term (1970–2018) historical climatic data for the locations of the PSPs were obtained from the global climatic databases WorldClim 2 (Fick and Hijmans 2017) and CRU-TS-4.03, bias corrected with WorldClim 2.1 (Harris et al. 2014). Monthly averages of mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) air temperatures, daily solar irradiance (S_R), total rainfall (R_F), vapour pressure and wind speed (W) were obtained for the period from 1970 to 2018. The monthly diurnal temperature range (DTR) was computed as the difference between T_{max} and T_{min} of each month. Monthly mean vapour pressure deficit (VPD) was computed as the difference between saturation vapour pressure and actual vapour pressure according to Allen et al. (1998). Monthly means of T_{min}, T_{max}, T_{mean}, DTR, VPD, S_R and W during the above period were used to compute their long-term averages for the respective PSPs. Mean annual R_F for the 1970–2018 period was computed by averaging the monthly totals and summing them over the 12-month period. Soil water deficit (SWD) was computed separately for each PSP on a monthly basis for the period from January 1990 to December 2018, using the soil water deficit model of Malhi and Wright (2004). For each PSP, the maximum monthly SWD (SWD_{max}) and maximum cumulative SWD ($CSWD_{max}$) were computed as indices of climatological drought.

Statistical analysis

Altitudinal trends of the measured and calculated variables were determined by linear and quadratic regression analysis using SAS Studio (SAS® Studio. SAS Institute Inc., Cary 2021). Multiple linear regression analysis was used to determine the influence of climatic variables on selected vegetation growth and diversity parameters. Several multiple regression models with different combinations of climatic variables as independent variables were run. The best-fitting model was selected based on the following criteria: (a) higher R^2; (b) higher Adjusted-R^2; (c) lower Akaike Information Criterion (AIC);

(d) lower Root Mean Square Error (RMSE); (e) absence of multicollinearity as indicated by a variance inflation of less than 10 for all independent variables; (f) statistical significance of the model at $p < 0.05$. Standardized regression coefficients (i.e., standardized change in the dependent variable per unit change in the standardized independent variable) were used to assess the influence of each climatic variable on a given vegetation parameter. A higher standardized coefficient, irrespective of its sign, indicated a greater influence and vice versa.

Results

Variation of climate with altitude

Long-term means of maximum (T_{max}), minimum (T_{min}) and average (T_{avg}) annual temperatures decreased with increasing altitude (Table 1). In contrast, the diurnal temperature range (DTR) increased with increasing altitude. Although long-term annual total rainfall (R_F) showed an overall decreasing trend with altitude, the R_F tended to level-off around a minimum of 1900−2000 mm y^{-1} from 1800 m asl upwards. Even though atmospheric vapour pressure decreased with increasing altitude, the vapour pressure deficit (VPD) did not show an altitudinal trend. Monthly maximum soil water deficit (SWD_{max}) and cumulative soil water deficit ($CSWD_{max}$) increased with increasing altitude.

Table 1
Long-term (1970−2018) climate of the permanent sampling plots (PSPs)

PSP	Alt. (m)	T_{avg} (ºC)	T_{max} (ºC)	T_{min} (ºC)	DTR (ºC)	R_F (mm y^{-1})	S_R (MJ m^{-2} d^{-1})	V_P (kPa)	VPD (kPa)	W (m s^{-1})	SWD_{max} (mm month⁻¹)	$CSWD_{max}$ (mm)
KDN1	117	26.40	29.52	23.57	5.95	3670	18.945	2.83	0.71	2.3	7.01	10.73
KDN2	174	26.18	29.14	22.98	6.16	3858	18.833	2.75	0.67	2.3	5.85	9.49
PTD2	509	24.15	27.49	20.99	6.50	3899	18.496	2.17	0.97	1.9	6.06	9.70
PTD1	618	23.82	26.99	20.65	6.34	3911	18.330	2.00	0.98	1.9	6.06	9.70
ENS1	1042	21.56	24.84	18.32	6.51	3130	17.910	2.00	0.58	2.2	17.58	23.71
ENS2	1065	21.56	24.84	18.32	6.51	3130	17.910	2.00	0.58	2.2	17.58	23.71
RLG	1668	19.65	23.40	15.82	7.58	2796	17.731	1.75	0.43	1.8	15.04	27.43
HKG	1804	17.05	20.67	13.48	7.19	2024	17.688	1.75	0.25	2.0	28.29	48.61
PTG	2080	15.56	19.14	11.98	7.15	1949	17.460	1.17	0.64	1.9	36.28	66.55
HNP	2132	14.75	18.32	11.34	6.98	2049	17.398	1.17	0.55	2.1	42.21	73.93

Alt. − Altitude; T_{mean} − Long-term annual average, T_{max} − maximum and T_{min} − minimum temperatures; DTR − Diurnal temperature range; R_F − Annual total rainfall; S_R − Mean daily incident solar irradiance; Vp − Mean atmospheric vapour pressure; VPD − Vapour pressure deficit; W −Mean wind speed; SWD_{max}: Maximum monthly soil water deficit; Cumulative SWD_{max}: Maximum cumulative soil water deficit during consecutive months

KDN1, KDN2: Kanneliya Plot 1 and 2; PTD1, PTD2: Sinharaja-Pitadeniya Plot 1 and 2; ENS1, ENS2: Sinharaja-Enasalwatte Plot 1 and 2; RLG: Rilagala; HKG: Hakgala; PTG: Pidurutalagala; HNP: Horton Plains National Park

Vegetation diversity

In a total plot area of 10.851 ha, we enumerated 8027 trees having DBH ≥ 10 cm, belonging to 276 tree species from 145 genera and 69 families, with a total basal area of 445.37 m^2. The numbers of species, genera and families decreased linearly (p < 0.05) with increasing altitude (Figs. 2.a - c). Stem density decreased from low to mid-altitudes and then increased from mid- to high altitudes (Fig. 2.d). This trend fitted a negative second-order polynomial function, which became significant (p < 0.05) when the two outlying data points at 1668 m and 2080 m were excluded. Shannon-Wiener (H') and Simpson's (D1) diversity indices and species richness (R) decreased linearly (p < 0.001) with increasing altitude (Figs. 3.a – c). Even though Shannon-Wiener evenness of tree species also showed a linear decline (p < 0.05) with altitude, Simpson's evenness did not show a significant trend (Figs. 3.d - e).

Floristic composition

Across all plots, the most dominant plant families, based on the Importance Value Index (IVI), were Dipterocarpaceae (IVI = 39.97) followed by Callophyllaceae (14.79), Malvaceae (14.36) and Myrtaceae (13.81). However, family Dipterocarpaceae and Malvaceae were recorded only up to 1065 m whereas Callophyllaceae and Myrtaceae were present across the whole altitudinal range. Different altitude classes had different dominant plant families, *viz.* 0 to 400 m: Dipterocarpaceae (39.94), Malvaceae (23.22), Sapotaceae (20.71); 400 m to 800 m: Dipterocarpaceae (80.58), Calophyllaceae (38.35), Malvaceae (33.66); 800 to 1200 m: Dipterocarpaceae (64.66), Clusiaceae (21.25), Myristicaceae (20.66); 1200 to 1800 m: Magnoliaceae (30.74), Sapindaceae (29.92), Lauraceae (27.88); Above 1800 m: Lauraceae (38.30), Symplocaceae (37.65), Myrtaceae (34.46).

Across the 10 plots, the most diverse families, in terms of the number of species present, were Myrtaceae (23 species), Dipterocarpaceae (22), Rubiaceae (21) and Lauraceae (14). The diversity of Dipterocarpaceae was higher at the lower (i.e. < 400 m) and lower-mid (400–800 m) altitudes than at the mid altitudes (800–1200 m) (Fig. 4.a). In contrast, Lauraceae showed a higher diversity at altitudes above 1600 m than at lower and lower-mid altitudes. Diversities of Rubiaceae and Myrtaceae did not show clear patterns of variation with altitude. At the lower and lower-mid altitudes, the diversity of Dipterocarpaceae was greater than those of the other three families. A similar superiority in diversity was shown by Lauraceae at altitudes above 2000 m.

Myrtaceae, which was the most diverse family across the whole range of plots, was represented by 18 *Syzygium* species, four *Eugenia* species and one *Rhodomyrtus* species. Genus *Shorea* dominated the Dipterocarpaceae family with 14 species along with three from *Dipterocarpus*, two each from *Hopea* and *Stemonoporus* and one *Vateria* species. Representation of Family Lauraceae consisted of five species from genus *Actinodaphne*, four from *Cinnamomum*, two each from *Neolitsea* and *Litsea* and one from *Cryptocarya*. In contrast to the other three families, Rubiaceae was represented in the plots by a broader range of genera with two species each from *Gaertnera*, *Psychotria*, *Psydrax* and *Urophyllum* and one each from *Byrsophyllum*, *Canthium*, *Dichilanthe*, *Diplospora*, *Diyaminauclea*, *Hedyotis*, *Ixora*, *Nargedia*, *Saprosma*, *Tarenna*, *Timonius*, *Uncaria* and *Wendlandia*.

The most dominant plant genus across all plots was *Shorea* (IVI = 31.48), followed by *Syzygium* (11.37) and *Allophylus* (9.77). *Shorea*, which was observed up to 1065 m, was the most dominant genus in the altitude classes 0–400 m (33.39), 400–800 m (59.40) and 800–1200 m (63.27). *Magnolia* (29.60) was the most dominant genus at 1200–1800 m while *Symplocos* (36.28) was the most dominant above 1800 m. The three most diverse genera were *Syzygium*, *Shorea* and *Semecarpus* with 18, 14 and 11 species respectively across all 10 plots (Fig. 4.c). *Shorea* was present only up to 1065 m whereas *Syzygium* and *Semecarpus* were present across the whole altitudinal range.

Despite their greater diversity in terms of the number of species recorded, contributions from the four most diverse families to the total tree number in the plots ranged from 15% (at 117 m) to 43% (at 174 m and 2080 m) (Fig. 4.b). Similarly, contribution to the total tree population from the three most diverse genera ranged from 8.5% at 1804 m to

41.1% at 174 m (Fig. 4.d). This meant that other less diverse plant families and genera contributed a greater proportion of individuals to the total tree population in the plots.

The most abundant plant family across the whole range of altitudes was Dipterocarpaceae. At different altitudes, different plant families were the most abundant. Apocynaceae (11.75%) at 117 m, Dipterocarpaceae at 174 m (30.03%), 618 m (32.98%) and 1042 m (18.96%), Calophyllaceae (25.91%) at 509 m, Clusiaceae (14.20%) at 1065 m, Sapotaceae (21.76%) at 1668 m, Sapindaceae (24.17%) at 1804 m, Lauraceae (25.0%) at 2080 m and Symplocaceae (24.66%) at 2132 were the most abundant families which recorded the highest percentage of individuals.

In terms of the proportion of individuals, *Shorea* (10.32%) was the most abundant genus across all plots. At the plot level also, *Shorea* was the most abundant genus at 174 m (26.85% of the individuals), 618 m (30.24%) and 1042 m (18.91%) (Fig. 4.d). In the other plots, the most abundant genera were *Alstonia* (11.68%) at 117 m, *Mesua* (25.58%) at 509 m, *Garcinia* (14.08%) at 1065 m, *Palaquium* (21.76%) at 1668 m, *Allophylus* (24.14%) at 1804 m, *Neolitsea* (18.58%) at 2080 m and *Symplocos* (54.57%) at 2132 m.

The most dominant plant species differed in different altitude classes and belonged to different plant families (Table 2). Within the same altitude class also, the most abundant tree species differed in different sampling plots. Accordingly, at the individual plot level, the most abundant species were *Alstonia macrophylla* (11.75%) at 117 m, *Syzygium firmum* (9.81%) at 174 m, *Mesua thwaitesii* (17.49%) at 509 m, *Shorea affinis* (15.78%) at 618 m, *Shorea gardneri* (10.81%) at 1042 m, *Garcinia echinocarpa* (12.48%) at 1065 m, *Palaquium rubiginosum* (21.76%) at 1668 m, *Allophylus zeylanicus* (24.20%) at 1804 m, *Neolitsea fuscata* (18.64%) at 2080 m and *Symplocos bractealis* (17.91%) at 2132 m.

Table 2

The three most dominant species at different altitudinal classes along with their conservation status and endemism within one-hectare permanent sampling plots in tropical rainforests of Sri Lanka along an altitudinal gradient

Altitude (m)	Species	Family	Conservation Status	Endemism	RD[†]	RF	RBA	IVI
0–400	*Cullenia rosayroana*	Malvaceae	LC	Endemic	7.47	1.08	10.72	19.27
	Alstonia macrophylla	Apocynaceae	NE	Exotic	10.25	0.54	6.92	17.72
	Syzygium firmum	Myrtaceae	LC	Native	4.56	1.08	9.24	14.89
400–800	*Shorea affinis*	Dipterocarpaceae	VU	Endemic	10.33	1.74	12.52	24.59
	Durio ceylanicus	Malvaceae	LC	Endemic	9.25	1.74	13.02	24.01
	Mesua thwaitesii	Calophyllaceae	LC	Endemic	11.95	1.74	4.99	18.68
800–1200	*Shorea gardneri*	Dipterocarpaceae	VU	Endemic	5.46	1.72	28.37	35.56
	Shorea trapezifolia	Dipterocarpaceae	VU	Endemic	7.10	1.72	16.00	24.82
	Myristica dactyloides	Myristicaceae	LC	Native	6.91	1.72	8.51	17.14
1200–1800[‡]	*Magnolia nilagirica*	Magnoliaceae	VU	Native	3.25	1.22	24.53	29.00
	Allophylus zeylanicus	Sapindaceae	LC	Endemic	17.22	1.22	6.25	24.68
	Neolitsea fuscata	Lauraceae	VU	Endemic	9.84	1.22	10.15	21.21
Above 1800	*Ilex walkeri*	Aquifoliaceae	LC	Native	10.98	2.90	14.56	28.44
	Symplocos bractealis	Symplocaceae	EN	Endemic	11.47	2.90	8.20	22.57
	Rhododendron arboreum	Ericaceae	VU	Endemic	10.98	1.45	8.91	21.34

[†]RD - Relative Density; RF - kal; RBA - Relative Basal Area; IVI – Importance Value Index. EN – Endangered; VU – Vulnerable; LC – Least Concern; NE - Not evaluated. [‡] - The plot at HKG was included in this altitude category despite being at 1804 m

Out of the 276 tree species found in the 10 forest plots, 117 (42.4%) were present in only one plot (Table 3). Another 117 (42.4%) species were found in only 2–3 plots while 39 (14.1%) were present in 4–5 plots. There was no single species which was present across the whole altitudinal range. However, three species were recorded in six out of the 10 plots. These were *Cullenia rosayroana* and *Semecarpus gardneri* which were found in all plots from low (117 m) to mid (1065 m) altitudes and *Melicope lunu-ankenda* which was present from mid (1042 m) to high (2132 m) altitudes (Supplementary Fig. S1). Among the total of 276 tree species, there were 154 species that are endemic to Sri Lanka. In addition, there were 100 tree species that are native to Sri Lanka and four species categorized as exotics. Origin of 18 tree species could not be determined. Nearly one-third of the endemics, just over half of the natives and all exotics were found in only one plot. Among the endemic and native species, 40.9% and 45% respectively recorded only 2–10 individual trees across all plots (Supplementary Table S2). Notably, only one individual was found in 9.7% of the endemics and 21% of

the natives. In contrast, more than 200 individuals were recorded from four endemic species (*Shorea affinis, Cullenia rosayroana, Symplocos bractealis*, and *Neolitsea fuscata*) and one native species (*Ilex walkeri*).

Table 3
Distribution and endemism of tree species found in one-hectare permanent sampling plots within tropical rainforests of Sri Lanka along an altitudinal gradient

Number of plots in which a species is found					
	one plot	2–3 plots	4–5 plots	6 plots	Total
Species total	117 (42.4%)[†]	117 (42.4%)	39 (14.1%)	3 (1.1%)	276
Endemic spp.	50 (32.5%)	73 (47.4%)	29 (18.8%)	2 (1.3%)	154 (55.8%)[‡]
Native spp.	51 (51.0%)	38 (38.0%)	10 (10.0%)	1 (1.0%)	100 (36.2%)
Exotic spp.	4 (100.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	4 (1.4%)
Unidentified	12 (66.6%)	6 (33.3%)	0 (0.0%)	0 (0.0%)	18 (6.5%)

[†]% of total species in each category in terms of the number of plots present; [‡]% of total species for each category in terms of endemism.

Endemism of tree species

The numbers of endemic species and individuals were greater than the corresponding numbers of native species and individuals in a majority of plots (Supplementary Fig. S2). This difference was greater at lower altitudes. While the number of endemic species per plot showed a clear decline with increasing altitude, the number of native species per plot remained within a narrow range (10–30 species) across the whole range of altitudes. The number of endemic individuals per plot showed a negative second-order polynomial variation pattern with altitude (Supplementary Fig. S2.a), which was similar to the altitudinal variation of total tree density (Fig. 2.d). The corresponding number of native individuals per plot showed an increasing trend with altitude (Supplementary Fig. S2.b).

The plot-wise percentage of endemic tree species decreased with increasing altitude (Fig. 5.a). In contrast, the corresponding percentage of native tree species increased with increasing altitude (Fig. 5.b). At the individual tree level also, the percentage of endemics decreased (Fig. 5.c) while the percentage of natives increased with increasing altitude (Fig. 5.d).

Conservation status of tree species

The conservation status could be determined for 258 tree species out of the total of 276 found in the 10 plots. Accordingly, there was one species, *Eugenia fulva* (with four individuals), identified as 'Critically Endangered Possibly Extinct, CR(PE)' which was present in both plots at the mid-altitudes (1042 and 1065 m). There were three species which have been listed as 'Critically Endangered (CR)', *Palaquium zeylanicum* (32 individuals), *Syzygium kanneliyensis* (3 individuals) and *Eugenia sripadaense* (1 individual). These were found respectively at 117 and 174 m, 117 m and 1668 m. In fact, *Eugenia sripadaense* had hitherto been considered as a 'point-endemic' confined only to the Peak Wilderness Sanctuary in the Central Highlands of Sri Lanka (6°48'47"N, 80°29'04"E). This is the first record of its existence outside the above sanctuary. Among the rest of the tree species, there were 40 designated as 'Endangered (EN)', 79 listed as 'Vulnerable (VU)', 33 identified as 'Near Threatened (NT)' and 96 known as 'Least Concern (LC)'. There were also six species which are categorized as 'Not Evaluated (NE)'. Out of the three most dominant species identified for each altitude category (Table 2), at least two species were in the VU or EN conservation categories at altitudes above the 400–800 m

category. With the exception of *Magnolia nilagirica* which is a native species, all other VU or EN species identified as dominant were endemics.

At the plot level, the number endangered and above (≥ END), which included the conservation status categories CE-PE, CR and EN, varied from 2 at 618 m to 14 at 117 m with no clear variation pattern with altitude (Fig. 6.a). However, the percentage of ≥ END tree species, out of the total number of species showed an increasing trend at upper altitudes (> 1100 m) (Fig. 6.b). Within this increasing trend, the forest plot at 1668 m showed a substantial increase in the percentage of ≥ END species. The forest plot at 2132 m had the highest percentage of ≥ END species while that at 509 m had the lowest percentage. In contrast to the number of ≥ END species, the number of tree species categorized as vulnerable (VU) decreased with increasing altitude from 36 at 117 m to 9 at 2132 m. Both the absolute number of VU species and their percentage out of the total species in the plot were greater than the respective numbers and percentages of ≥ END species in 8 out of the 10 plots. The combined percentage of ≥ END and VU species, which represented the fraction of the tree population that required conservation effort, exceeded 33% in forest plots at all altitudes. It was greater than 45% in 7 out of the 10 plots while being greater than 50% in 3 out of those 7 plots. Two out of these 3 plots were located above 2000 m while the other was located at 174 m. The combined percentage NT and LC, which represented the fraction of the tree population that does not require a conservation effort at present, ranged from 43% (at 2080 m) to 57% (1042 m). Altitudinal variation of the absolute numbers of individuals classified in to the three conservation categories (i.e. ≥END, VU and NT + LC) (Fig. 6.c) showed both similarities and differences when compared to the corresponding variation in the number tree species (Fig. 6.a). The similarity was between the altitudinal variations of ≥ END species numbers (Fig. 6.a) and ≥ END individual numbers (Fig. 6.c), where there were no clear altitudinal patterns for both. On the other hand, while there were clear reductions with increasing altitude in the percentages of VU and NT + LC species numbers (Fig. 6.a), such a pattern was not observed in their corresponding numbers of individuals (Fig. 6.c). However, the altitudinal variation patterns in the percentages of species (Fig. 6.b) and individuals (Fig. 6.d) were similar for the three conservation categories.

Percentages of ≥ END and VU species showed significant negative quadratic trends with increasing altitude (Supplementary Fig. S3). Notably, ≥END species reached an estimated minimum at 654 m whereas the corresponding minimum for VU species occurred at the much higher altitude of 1531 m. The percentage of ≥ END individuals also showed a negative quadratic trend, with the estimated minimum occurring at 802 m. However, the corresponding percentage of VU individuals did not show a clear pattern. The percentage of NT + LC species showed a positive quadratic response to altitude, with the estimated maximum occurring at 1007 m. However, the corresponding percentage of NT + LC individuals did not show a clear trend.

Influence of climatic variables on selected vegetation and diversity parameters

The best-fitting multiple regression models that describe the influence of long-term mean climate on H and the percentages of endemic and ≥ END species are shown in Table 4. All three vegetation variables were influenced by DTR and either $CSWD_{max}$ or R_F. Shannon-Wiener H decreased with increases in both DTR and $CSWD_{max}$. Standardized regression coefficients showed that the influence of DTR on H was stronger than that of $CSWD_{max}$. The percentage of endemic species decreased with increasing DTR, but increased with increasing R_F, with the influence of R_F being stronger. The % of ≥ END species increased with increases in both DTR and $CSWD_{max}$, where the influence of $CSWD_{max}$ was stronger.

Table 4
Coefficients of the best-fitting multiple regression models between selected vegetation variables and long-term (1970–2018) annual means of climatic variables

Vegetation variable	Intercept	DTR (°C)	CSWD$_{max}$ (× 10^{-3} mm)	R$_F$ (× 10^{-3} mm y^{-1})	R^2	Adj. R^2	AIC	RMSE	p
H	6.341	-0.459†	-4.863	.	0.866	0.828	-36.06	0.146	0.0009
		(-0.67)‡	(-0.34)						
%End-Sp	75.751	-6.112	.	8.16	0.619	0.511	44.56	8.219	0.0340
		(-0.27)		(0.56)					
%Endg-Sp	-16.503	3.884	179.61	.	0.642	0.540	34.56	4.984	0.0274
		(0.27)	(0.59)						

†Regression coefficient in measured units; ‡Regression coefficient in standardized units; H: Shannon-Wiener diversity index; %End-Sp: Percentage of endemic species; %Endg-Sp: Percentage of species categorized as 'Endangered' and above (>= END); DTR: Diurnal temperature range; R$_F$: Mean annual rainfall; CSWD$_{max}$: Mean annual cumulative maximum soil water deficit. AIC: Akaike Information Criterion; RMSE: Root mean squared error; p: Probability of significance of the regression model

Discussion

Our results show that community-scale tree diversity and species richness decrease with increasing altitude in the tropical rainforests in Sri Lanka, which are representative of those in South Asia. This trend agrees with similar trends observed by Gentry (1988), Aiba and Kitayama (1999) Homeier et al. (2010) and Cirimwami et al. (2019). In contrast, both Lieberman et al. (1996) and Clark et al. (2015) observed mid-altitude peaks of diversity. However, our results support the conclusion of Gentry (1988) that there is no 'mid-elevation bulge' in the diversity of tropical rainforests.

The observed decreases of tree diversity and species richness were caused by decreased numbers of families, genera and species with increasing altitude. These decreases indicate that environmental constraints at higher altitudes imposed a limitation on the colonization of tree species. For example, the reduction of mean annual air temperature from 26.4°C to 14.75°C across the altitudinal range (Table 1), probably exerted a restriction on the ecological range of most tree taxa of these tropical rainforests, which have evolved under and adapted to tropical climates. This agrees with Janzen (1967)'s hypothesis that tropical species find it harder to colonize and survive at higher altitudes and also supports our Hypothesis 2. However, it is notable that despite the reduction in taxon numbers and diversity, the individual tree numbers increased with increasing altitude from 1000 m onwards. This showed that a smaller number of tree taxa were able to tolerate the environmental constraints and proliferate at higher altitudes. A similar increase in stem density was observed at the highest altitude (2800 m) in the studies of Lieberman et al. (1996) and Clark et al. (2015).

Altitudinal ranges of the most diverse families contributed to the decreased community-scale diversity with altitude. The most diverse family in the lower altitudes (Dipterocarpaceae) was more diverse (i.e. a greater number species) than the most diverse families in the higher altitudes (Lauraceae, Rubiaceae and Myrtaceae) (Fig. 4.a), thus driving the reduction in diversity indices with altitude. Furthermore, whereas distribution of the latter three families extended into the lower altitudes, the distribution of Dipterocarpacea did not extend up to the higher altitudes. Similar variations in the most diverse plant genera (Fig. 4.b) have further contributed to this trend. The most diverse genus at the lower altitudes, *Shorea*, had higher species numbers at low altitudes than the most diverse genera at the higher altitudes, *Syzygium* and

Semecarpus. Furthermore, whereas *Syzygium* and *Semecarpus* extended to lower altitudes and increased the diversity there, *Shorea* did not extend beyond mid altitudes. Lieberman et al. (1996) and Aiba and Kitayama, (1999) also observed changes in the distribution of families across altitudes. Agreeing with our observations, Aiba and Kitayama (1999) also observed Dipterocarpaceae and mostly *Shorea* species dominating their lower altitude (700 m) plots whereas Myrtaceae and *Syzygium* were among the dominant families and genera at higher altitudes respectively.

The observation that 42.4% of the 276 species recorded were present in only one plot while 84.8% were present in only three-or-lesser number of plots (Table 3) indicates a high degree of niche differentiation, thus supporting our Hypothesis 1. However, the respective distributions of the three species which had the broadest altitudinal range (Supplementary Figure S1) show that a small minority of tree species were able to colonize a wider range of climates and soils, thus supporting our Hypothesis 3. It is notable that the two species whose range covered the low to lower-mid altitudes (i.e. *Cullenia rosyrona* and *Semecarpus gardneri*) are present in the sub-canopy. Therefore, it is likely that the partial shade in their microenvironment has insulated these sub-canopy species from the higher temperatures that are prevalent in this altitudinal range, thus enabling them to colonize a wider altitudinal range. In contrast, *Melicope lunu-ankenda*, the species which has the broad altitudinal range covering the mid to higher altitudes, occupies the sub-canopy at the mid altitude but occupies the canopy at high altitudes. This provides further support to our hypothesis (i.e. Hypothesis 2) that temperature could be a strong climatic determinant of species distribution as the lower temperatures at higher altitudes may have enabled *Melicope lunu-ankenda* to move from the sub-canopy to the canopy. It is also possible that *Melicope lunu-ankenda* had greater tolerance to the substantially lower temperatures and higher soil water deficits at the higher altitudes (Table 1), which enabled it to extend upwards. In contrast, *Cullenia rosyrona* and *Semecarpus gardneri* may not have had adequate adaptive mechanisms for cold and drought tolerance to extend to higher altitudes.

The high degree of endemism at the lower altitudes (Supplementary Fig. S2) and its observed decrease with increasing altitude (Figs. 5.a and c) indicate that most endemics have probably evolved under and adapted to warmer humid tropical climates, thus supporting our Hypothesis 2. A reduction of the percentage of endemics with increasing altitude (Fig. 5.c), in parallel with the reduction of total species number (Fig. 2.b), demonstrates an inability of the lowland-adapted species to establish at higher altitudes or long-term extinction of endemic species with increasing altitude (Anderson 1994). As decreasing temperature is the environmental factor that is most closely linked to increasing altitude, the narrow range of thermal tolerance of endemics in these tropical rainforests most likely caused their decline with increasing altitude. The observation that more than 50% of the endemic species have 10-or-less individuals across the whole range of plots and altitudes (Supplementary Table S2) not only highlights their extreme niche differentiation, but also their vulnerability to extinction. Accordingly, urgent conservation efforts are needed for these rare endemics.

Conservation status of tree species in our plots indicates the high vulnerability for extinction for a majority tree species in these tropical rainforests. Of particular concern is the increasing trend of ≥ END species at altitudes above 650 m (Fig. 6 and Supplementary Fig. S3.a). One possible cause for this could be the long-term increases in air temperature. The central highlands of Sri Lanka where the high-altitude plots of our study are located have experienced a significant increase in decadal mean annual temperature over the last 150 years (De Costa 2008). Most species in the high-altitude plots, which probably evolved under and adapted to cooler temperatures, may not have evolved physiological mechanisms and morphological features to withstand the rapid increase in temperature that they have experienced. Absence of mechanisms to tolerate increased frequency and intensity of drought could also have contributed to the increased percentages of ≥ END species and individuals at higher altitudes. De Costa (2008) have shown significant declining trends in precipitation in the central highlands of Sri Lanka. Even though this is a region of high annual precipitation (> 2000 mm), it is probable that the frequency and duration of dry periods have increased. This would have endangered the existence of many high-altitude tree species. Most of these species have evolved and adapted to continuously wet environments without pronounced dry periods and may not have adequate mechanisms to conserve water or tolerate drought. The observed reduction of endemic species at higher altitudes (Fig. 5 and Supplementary Figure S2) agrees with

the conclusion of Jansson (2003) that there would be fewer endemic species in areas which have experienced greater historical climate change.

The decreasing percentage of VU species from low altitudes up to *ca.* 1500 m (Fig. 6.b and Supplementary Fig. S3.b) indicates that despite their evolutionary adaptability to higher temperatures, many tree species that inhabit low altitudes in a higher temperature regime, are vulnerable to the increased temperature and frequency of drought (De Costa 2008). This vulnerability decreases with increasing altitude and the cooler temperature regime so that climate warming in the recent past probably has not increased temperatures at mid-altitudes beyond the tolerance range of a majority of tree species. The percentage of VU species begins to show an increasing trend above 2000 m, probably because of the narrow range of ecological tolerance of the high-altitude species. The relatively cold-adapted species at the higher altitudes are finding it difficult to adapt to the rapid temperature increase and increased frequency of drought in the recent past. It is possible these species could shift from the VU status to the END status in the near- to medium-term future due to continued climate change.

Multiple regressions of vegetation indices against long-term climatic variables (Table 4) confirmed the strong influence of temperature and water availability in determining the floristic composition of tropical rainforests across altitudinal gradients. Importantly, this analysis demonstrates the role of the day-night temperature differential (DTR), which increased with altitude (Table 1). The decreasing tree diversity and endemic percentage along with increasing $\geq$ END percentage with increasing DTR confirm the narrow thermal range of most tree species in the tropical rainforests of Sri Lanka and South Asia. Similar decreasing trends of the above vegetation indices with either $CSWD_{max}$ or R_F provides evidence of a narrow tolerance range for water availability as well. Thus, we identify lower thermal and drought tolerances as major drivers of increased climate vulnerability of Sri Lankan and South Asian rainforests and their tree taxa, especially at higher altitudes.

The absence of a mid-altitude peak in tree diversity disproves our Hypothesis 4 so that there is no overlapping region where warm-adapted low-altitude taxa and cold-adapted high-altitude taxa co-exist. This re-affirms our Hypothesis 1 of significant niche differentiation. The increasing trend of $\geq$ END endemics at higher altitudes along with the increase of VU species at high altitudes clearly indicates that a greater conservation effort is needed at the higher altitudes. This disproves our Hypothesis 5 of equal conservation importance across all altitudes.

Conclusions

We conclude that tree diversity of tropical rainforests in Sri Lanka, which are representative of those in South Asia, decreases with increasing altitude and that this is most likely driven by the absence of cold and drought tolerance in a majority of tree species, which have primarily evolved under and adapted to warm climates. Our results also demonstrate the high degree of habitat differentiation and endemism in these tree communities. The high percentage of endangered and vulnerable species in this ecosystem highlight the need for a substantial conservation effort. The altitudinal trend in the $\geq$ END species shows that the conservation efforts are most urgently needed at the high (> 1500 m) and mid (*ca.* 1000 m) altitudes. However, in view of the high percentage of VU species, the low altitudes ($\leq$ 500 m) cannot be ignored in medium- and long-term conservation planning.

Declarations

Data availability

The datasets generated during the current study are available from the corresponding author and Nimalka Sanjeewani on reasonable request.

Competing interests

The authors declare no competing or financial interests.

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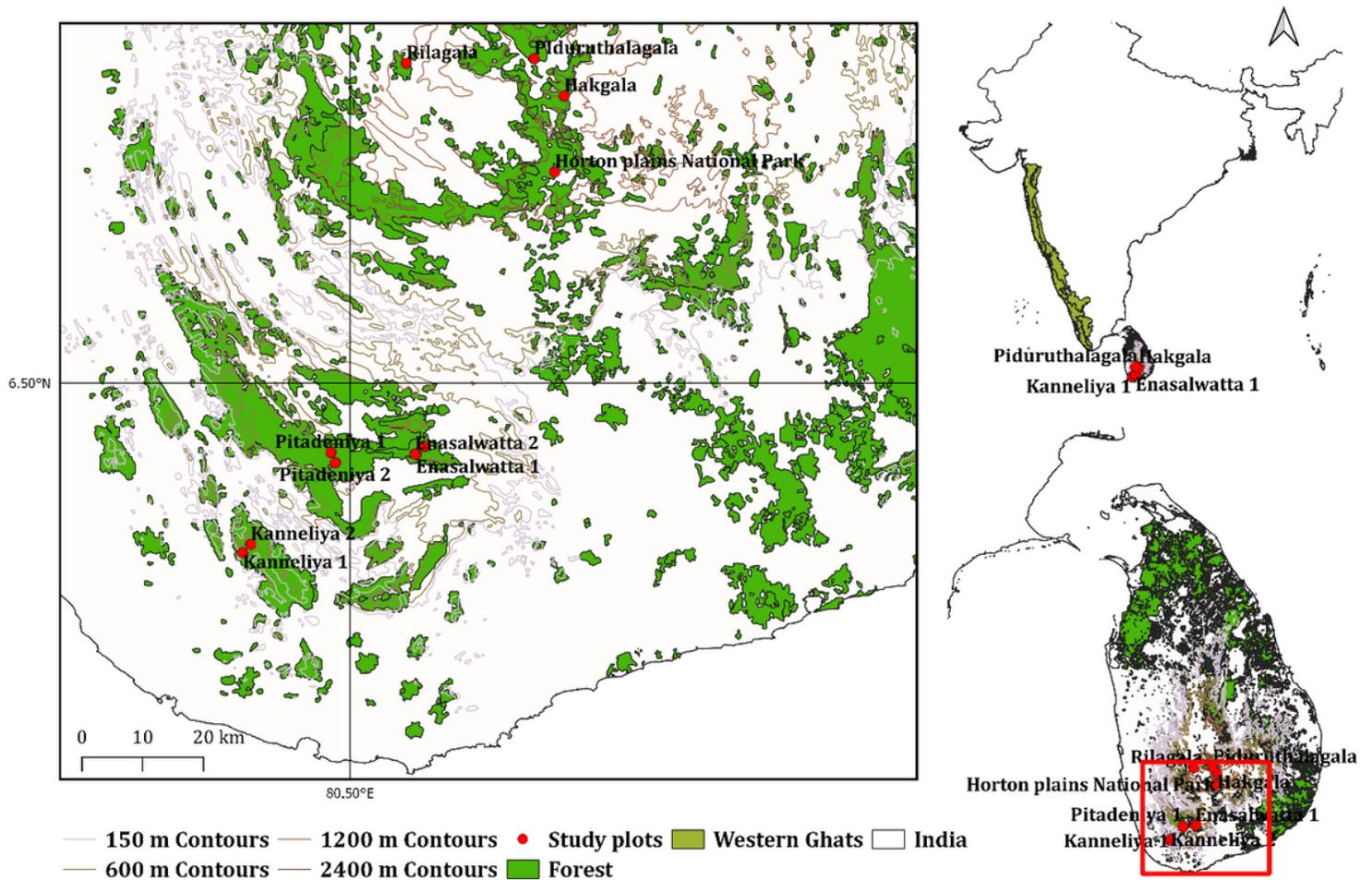
Figures

Figure 1

Permanent sampling plots of the present study located at different altitudes in tropical rain forests of Sri Lanka. Kanneliya Plot 1 (KDN1 at 117 m asl) and Plot 2 (KDN2 - 174 m), Sinharaja-Pitadeniya Plot 1 (PTD1 - 618 m) and Plot 2

(PTD2 - 509 m), Sinharaja-Enasalwatte Plot 1 (ENS1 – 1042 m) and Plot 2 (ENS 2 – 1065 m), Rilagala (RLG - 1668 m), Hakgala (HKG -1804 m), Piduruthalagala (PTG - 2080m) and Horton Plains (HNP – 2132 m)
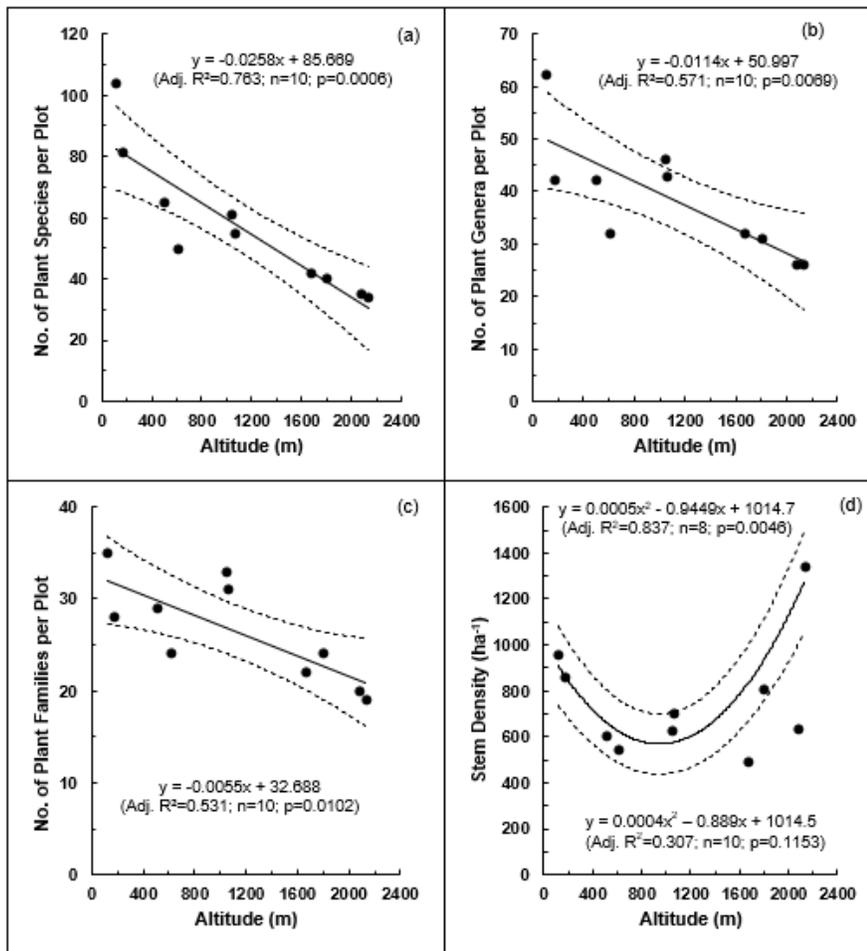
Figure 2

Variation of the numbers of: (a) plant species; (b) plant genera; (c) plant families and (d) stem densities with altitude in permanent sampling plots in selected tropical rainforests in Sri Lanka. Dotted curves show the 95% confidence limits of the fitted linear (a-c) and polynomial (d) regressions. In (d) the curve has been fitted after excluding the two outliers at 1668 and 2080 m. The regression equations with- (bottom) and without (top) outliers are shown
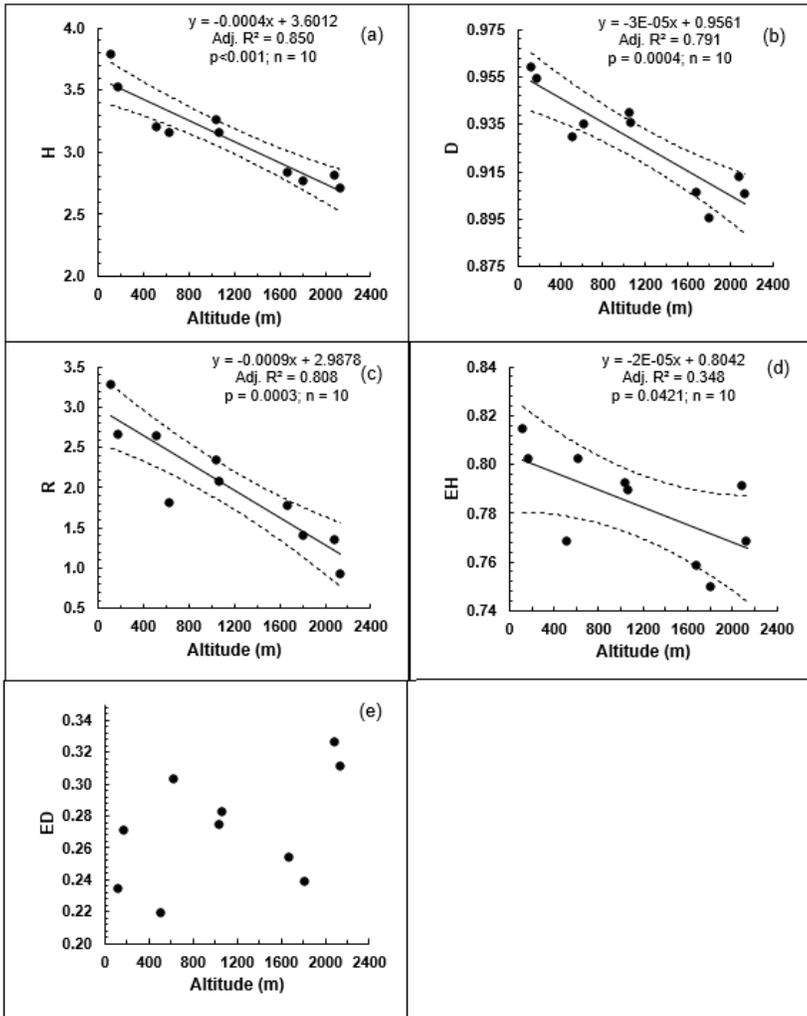
Figure 3

Variation of the (a) Shannon Weiner diversity index (H), (b) Simpson's diversity index (D), (c) Species richness R), (d) Shannon evenness (EH) and (e) Simpson's evenness (ED) among the tropical rainforests in Sri Lanka along an altitudinal gradient
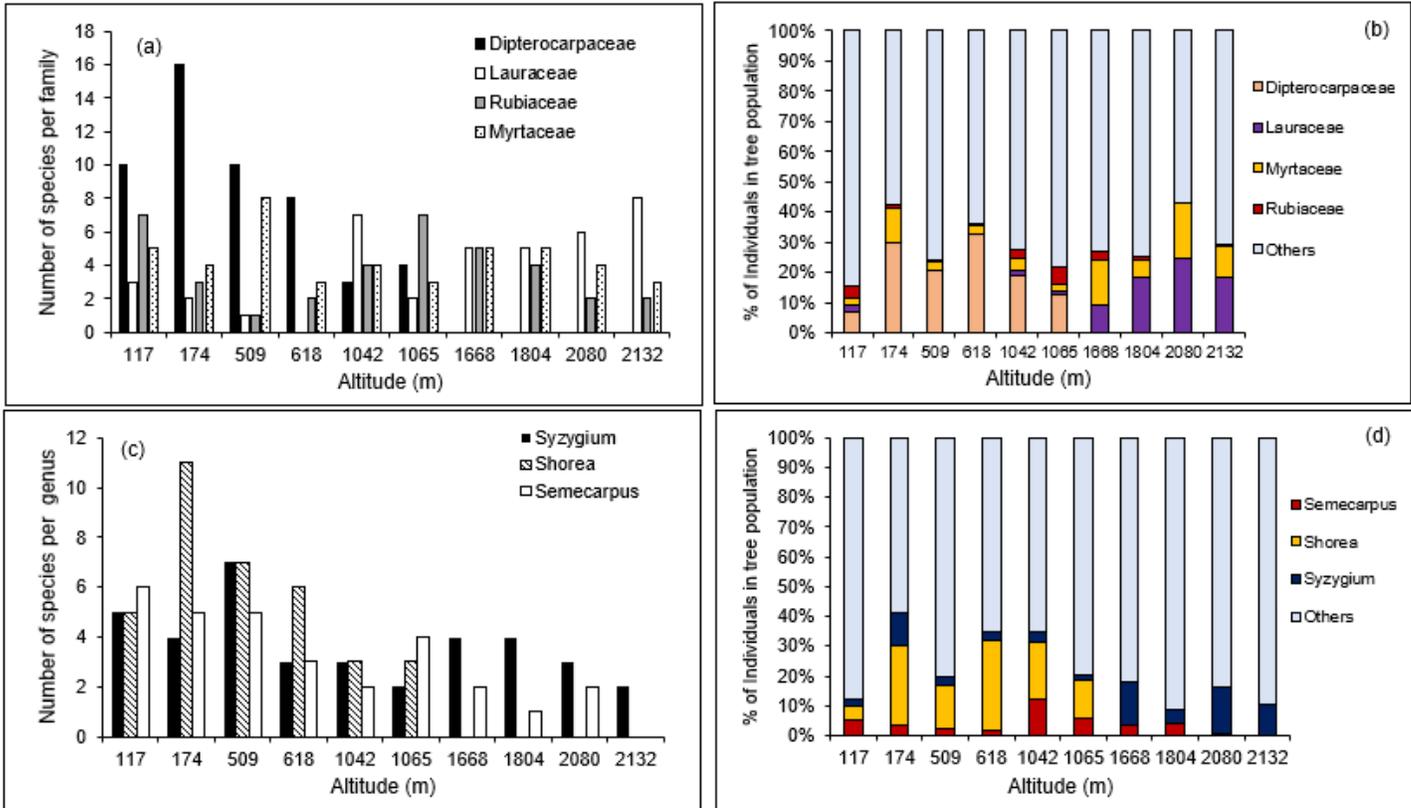
Figure 4

The four most diverse plant families (a) and the three most diverse genera (c) and their percentage contributions to the total tree population in each sampling plot (b and d) in selected tropical rainforests in Sri Lanka across an altitudinal gradient
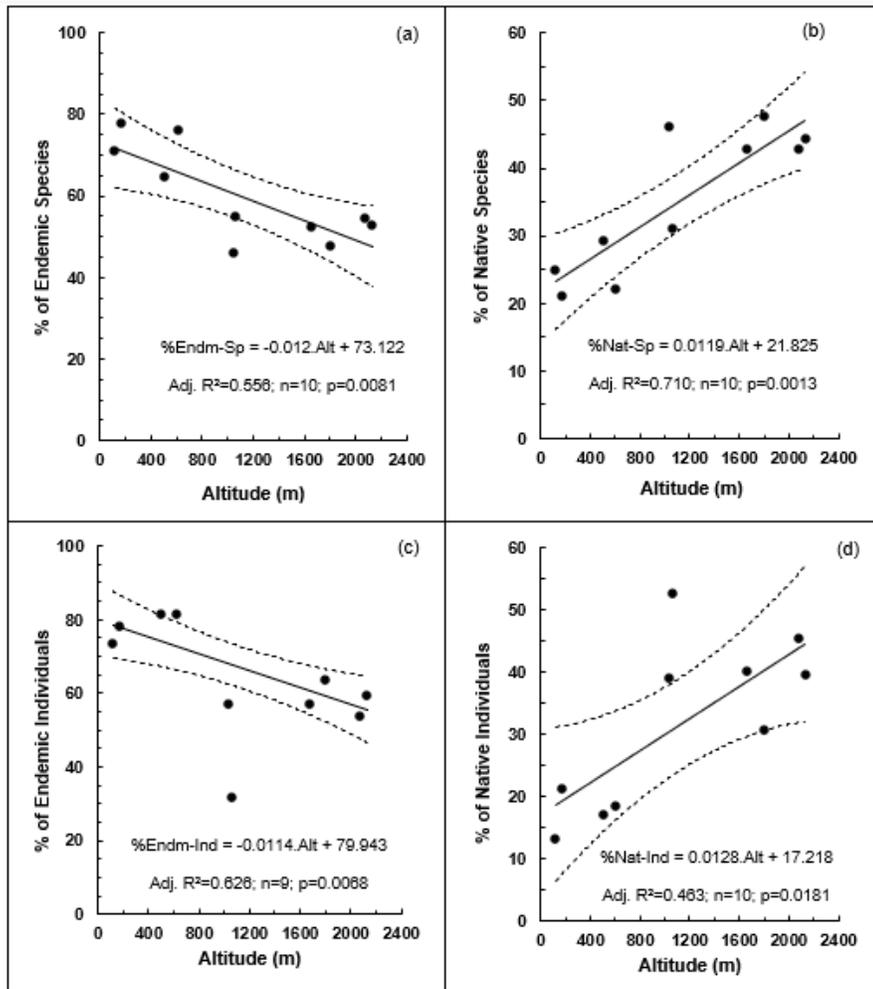
Figure 5

Variation of the per-plot percentages of: (a) endemic plant species; (b) native plant species; (c) endemic plant individuals and (d) native plant individuals with altitude in permanent sampling plots in selected tropical rainforests in Sri Lanka. Dotted curves show the 95% confidence limits of the fitted linear regressions. In (c) the linear regression has been done after excluding the outlier at 1065 m. Alt: Altitude.
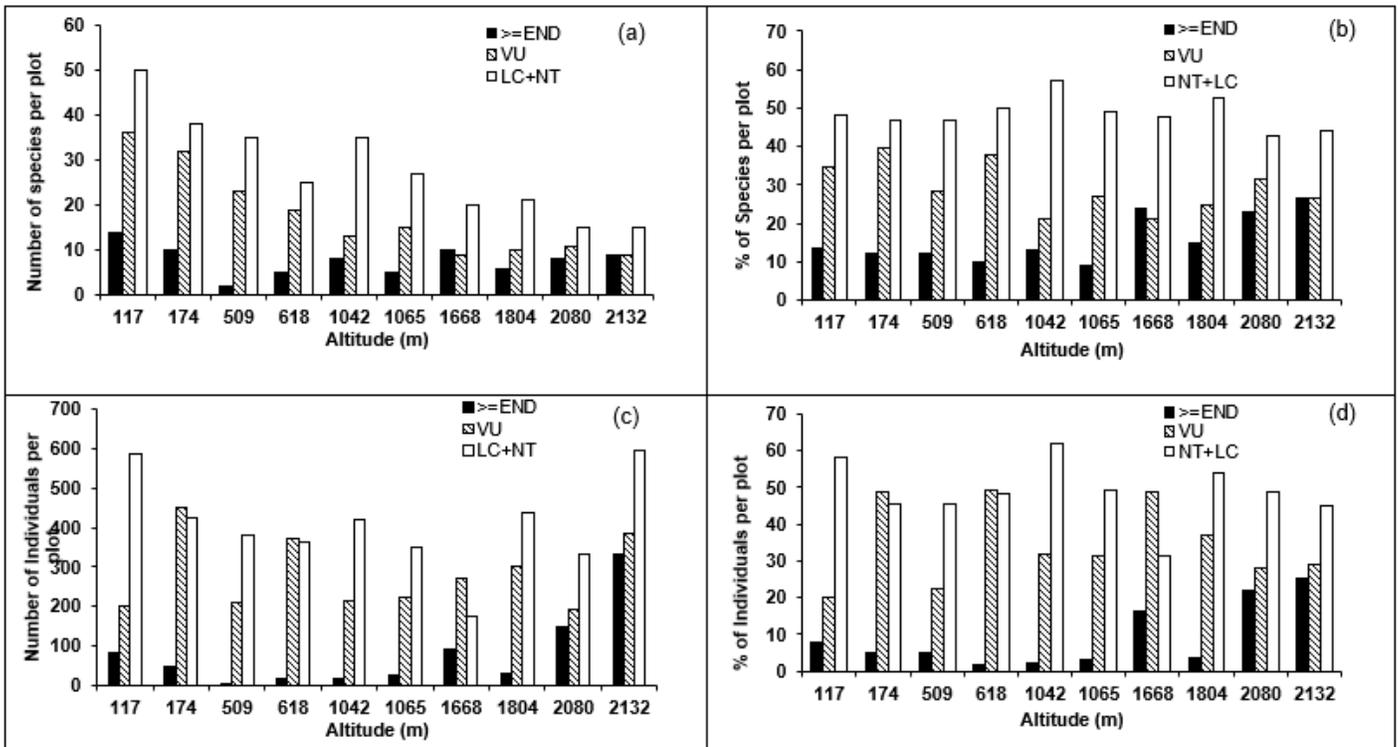
Figure 6

Conservation status of the (a) number of species (b) number of individuals (c) percentage of species (d) percentage of individuals in permanent sampling plots of selected tropical rainforests in Sri Lanka along an altitudinal gradient. >= END: Endangered and above (i.e. Endangered, Critically-Endangered and Critically-Endangered and Nearly-Extinct); VU: Vulnerable; LC+NT: Least Concern and Near-Threatened.

Supplementary Files

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