RESEARCH ARTICLE

Diversity and distribution of vines in the tropical forests of Nilgiri Biosphere Reserve, India

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This article elucidates the diversity and distribution of vines (climbing plants) in a biodiversity-rich part of Nilgiri Biosphere Reserve in the Western Ghats of India. A total of 59 vine taxa belonging to 44 genera of angiosperm families were recorded from the heterogeneous forest landscape of the Reserve. The lianas encountered in the six vegetation types fall under six climber categories of which twining was the chief climbing mechanism, both in terms of richness and abundance. With regard to species abundance, there was negative correlation between vines and trees. The coefficient of variation in species distribution among the different vegetation types was used to identify the oligarchy among vine species and establish that vines in different vegetation types are dominated by limited set of species. At the same time, 47% of the vines occurred in only one of the six vegetation types, which supports the environmental determinism hypothesis.

Keywords: Habitat preference, oligarchy hypothesis, spatial distribution, species richness, vines.

CLIMBING plants or vines ascend to the canopy of other plants with the help of their architecture. Almost one-third of the plant families include vines[1] and contribute significantly to the functioning of any forest ecosystem. The climbing habit has evolved several times during the process of evolution and has boosted plant diversification[2]. They influence forest trees in their demography and ecophysiology[3,4]. Unlike trees, vines need relatively less structural support and hence they can allocate more of the resources for vegetative growth and reproduction. Thus, they typically have very high canopy–stem ratio, which results in a higher proportion of photosynthetic biomass compared to most of the woody plants[5]. Vines are also adapted for survival from treefalls because of their anomalous stem anatomy, which reduces stem breakage and accelerates repair of damaged vascular tissue[6]. Vines differ from other structural parasites (epiphytes and hemiepiphytes) as they remain rooted to the ground throughout their life. Vine diversity is maximum in the lowland tropics, which declines with increase in latitude and elevation[7]. In both tropical and temperate ecosystems, vines proliferate along the whole light gradient[8]; but a few vines can survive in shaded environment also[9,10]. As they contribute a lot to the species diversity, structure and dynamism of tropical forests[11], it would be interesting to know how vine communities are dispersed over geographically different environmental gradients. Almost 90% of vine species occur within the tropics[12].

The abundance and distribution of vines usually depend on abiotic factors, including elevation, rainfall and seasonality, soil fertility and level of disturbance of the formation. Vine density also has positive correlation with the density of trees in the diameter class of 1 and 10 cm, probably because of their suitability as trellises[13]. Their abundance is related to availability of support rather than nutrients or light availability[14]. Vine density and basal area may also be more in fertile soils[1] even though a clear relationship with soil fertility remains elusive[15,16]. Areas with a pronounced dry season and low annual rainfall generally have high liana densities[17], perhaps because lianas, due to their deep root systems and efficient vascular systems, have a competitive advantage over other life-forms in seasonally dry areas[18]. Vines thrive where there is less tree competition and such conditions are characteristic of disturbed habitats. Annual rainfall and seasonality variations together explain more of the differences in species richness than any other independent variable. There is a steady increase in species richness as annual rainfall increases and a steady decrease in species richness as the average length of the dry season increases[19]. As in the case of trees, edaphic specialization may be one mechanism by which the diversity of vine species is maintained in the tropical forests[20] and their oligarchic dominance results from ecological superiority of the dominant species[21].

Recent studies suggest that vines have increased dominance in tropical forests[22,23], and there are certain evidences suggesting that the same may be occurring in temperate forests also[24]. Several factors could be driving this, including a direct response to the increased atmospheric CO_2 levels, which may have a disproportionately strong effect on the vines[25–27]. Increased turnover of

trees[28], the recent warming of the tropics[29] or even increase in hunting intensity could benefit wind-dispersed vines at the expense of animal-dispersed trees[30]. Because of their role in forest dynamism, increased dominance of vines may in turn lead to changes in the tree floristic composition (biodiversity impact) and reduce the carbon sequestration capacity (carbon cycle and climate impact) of tropical forests[31]. Determination of factors which control vine population may therefore be an essential prerequisite to predict the impacts of climate change in the tropical forests.

In the present study, the term vines is applied to all perennial climbers (includes both soft and woody climbers or lianas) like twiners, scramblers, tendril climbers, root climbers, hook climbers and climbing palms which start their life cycle on the forest floor and excludes herbaceous or thin vines. Most of the inventories on tropical vines were from the Neotropics[32–35] and Southeast Asia[36–38] and only a few are available from South Asia, especially from the Western Ghats of India[17,39,40]. In the present study, emphasis is given to the diversity and spatial distribution pattern of vines in six different tropical forest formations of the heterogeneous landscape of Nilgiri Biosphere Reserve area. The study aims to test the hypothesis[21] that majority of species of different vegetation types are dominated by limited number (oligarchy hypothesis) and also to assess their restricted distribution pattern in different vegetation types (environmental determinism hypothesis). Based on these two hypotheses, the following objectives are addressed: (i) to assess the species diversity (including richness and abundance) and distribution of vines in relation to the supporting tree density, (ii) to assess the relationship between abundance (density) and distribution (frequency) of species in different vegetation types, (iii) to find out relative contribution of light-demanding and shade-tolerant species in different forest formations of the landscape, and (iv) to identify oligarchy in vines and also examine their habitat preferences.

Methods

Study area

The study area is the New Amarambalam Reserve Forest, which is a heterogeneous landscape with representation of all the major forest types of the Western Ghats of India. It forms part of the core area of Nilgiri Biosphere Reserve within Kerala. The area extends to about 265 sq. km between 11°14′N and 11°24′N lat. and 76°11′E and 76°33′E long. The natural vegetation types of the area are Southern tropical moist deciduous forests (MOIS), West coast tropical semi-evergreen forests (SEMI), West coast tropical evergreen forests (EVER) and Southern subtropical broadleaved hill forests

(SUBT), Southern subtropical hill savannahs (SAVA), Southern montane wet temperate forests (MONT) and Southern montane temperate grasslands (GRAS)[41]. Out of the seven vegetation types, MOIS – a monsoon forest type (depends exclusively on seasonal monsoon showers and trees in the forest shed their leaves completely during summer) – is situated in the foothills of the Ghats, while the other forest types are at higher elevation forming part of the rainforest (receiving rain throughout the year due to higher elevation and topography and trees do not shed their leaves completely[42]). Owing to frequent fire and absence of tree species, vines are not found in GRAS. The different vegetation types are located at an altitudinal range 40–2600 m amsl (Table 1). The temperature of the area ranges between 17°C and 37°C and the diurnal variation seldom exceeds 16°C. In the higher elevations, during the winter months of December and January, temperature goes down to almost 0°C. The area receives an average rainfall of above 2600 mm, which sometimes goes up to 6000 mm in the hills. Major portion of the precipitation is from the southwest monsoon, which starts from June and lasts till the end of September. The monsoon precipitation is maximum along the western, southwestern and northwestern aspects of the hill slopes. Apart from this, the higher altitudes of the Ghats receive rain almost throughout the year, mainly due to their topographic features.

Vegetation sampling and analysis

Vines recorded from the study area were categorized as scramblers, twiners and root, hook, tendril and grapnel-like climbers[43]. Vines which grow and reproduce in the understorey and those rarely reaching the tree canopy were considered as shade-tolerant, which were restricted to rainforests, while vines that cover the tree canopy are considered as light-demanding species seen in both monsoon forests and rainforests. Vegetation analysis was conducted during 2001–2003 in a total of area of 23 ha with 259 sample plots. In each vegetation type 45 plots (4 ha) were laid, except for SAVA where the complete area was sampled in 34 plots. For 1 ha sampled area, eleven 30 m × 30 m size plots were laid. These plots were distributed at random in order to cover all the microclimatic conditions within each forest type. For both vines and trees, girth at breast height (gbh) was measured at 1.3 m above the ground level. The vines were grouped into two growth phases, i.e. large vines (≥ 10 cm gbh) and small vines ($\geq 1 < 10$ cm gbh). All the vines and trees above 10 cm gbh were enumerated from the sample plots. Within each 30 m × 30 m plot, ten random sub-plots of 2 m × 2 m size were designated for recording details of small vines. The altitudes of different plots were also recorded using a pocket altimeter with a sensitivity of 20 m and the slope was measured using a multimeter.

Table 1. Structural parameters of vines (≥10 cm gbh) and corresponding environmental variables in different vegetation types of the study area. There are no vines above 10 cm gbh in the vegetation types like SAVA and MONT

Vegetation types*	Basal area (m^2 ha^{-1})	Shannon index	Simpson index	Altitude range (m)	Rainfall (mm)	Mean temperature in the coldest month (°C)	Slope (%)
MOIS	0.32	0.98	0.57	40–400	1000–1500	28	0–10
SEMI	0.74	2.92	0.09	450–650	2500–3500	24	10–30
EVER	0.79	2.67	0.10	700–1200	3500–5000	22	20–45
SAVA	–	–	–	1000–1500	3500–5000	25	20–40
SUBT	0.19	1.86	0.18	1300–1600	5000–6000	13	30–75
MONT	–	–	–	1800–2500	5000–6000	9	30–70

*MOIS, Southern tropical moist deciduous forests; SEMI, West coast tropical semi-evergreen forests; EVER, West coast tropical evergreen forests; SUBT, Southern subtropical broadleaved hill forests; SAVA, Subtropical hill savannahs; MONT, Southern montane wet temperate forests.
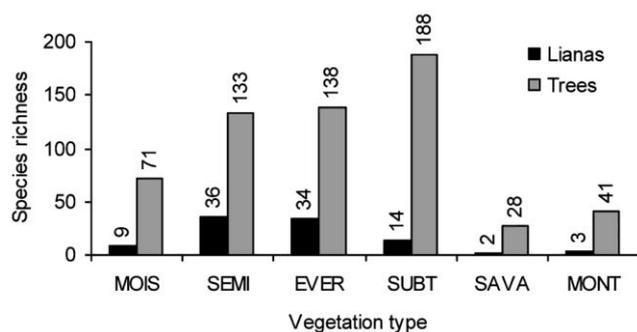

Figure 1. Species richness of vines and trees in different forest types of the study area showing their negative correlation. MOIS, Southern tropical moist deciduous forests; SEMI, West coast tropical semi-evergreen forests; EVER, West coast tropical evergreen forests; SUBT, Southern subtropical broad leaved hill forests; SAVA, Southern subtropical hill savannahs; MONT, Southern montane wet temperate forests.

To quantify and compare floristic composition among habitats, vegetation parameters like density (number of individuals ha^{-1}), species richness (number of species), frequency and basal area were calculated. Also, Shannon index and Simpson index were arrived at for each forest type[44]. To assess species–individual relationship of different vegetation types, species–individual rarefaction curves (individual-based rarefaction) were generated in randomly selected 30 plots of 30 m × 30 m size. Rarefaction was used to study the richness of the community expected in a random sample of individuals based on census or collection.

Only individuals rooted within the plots were included in the analysis. The degree of dominance in different vegetation types was described and quantified by identifying the five most common species (the dominant taxa) of vines in each vegetation type and computing the density proportion of the stems in the vegetation types they accounted for. The extent to which different taxa were shared among the vegetation types was assessed. Proportion of light-demanding and shade-tolerant vines was also calculated. One-way ANOVA and LSD (a post-hoc test for multiple comparisons) were used to compare the richness, density and basal area of vines in different vegeta-

tion types. Pearson correlation was used to assess the relationship of vegetation parameters between vines and tree species of different vegetation types, using the statistical package SPSS (Version 16). For rarefaction, we used the statistical software Biodiversity Pro (http://www.smi.ac.uk/peter-lamont/biodiversity-pro). The co-efficient of variation (CV – standard deviation/mean for a species) was computed to understand whether there was oligarchy in vine species across the four vine-rich vegetation types. This would provide information on site differentiation with respect to species composition, i.e. whether species with a low CV regardless of absolute density are equitably distributed or those with a high CV show a high degree of variability in their distribution.

Results

Species diversity

A total of 59 species of vines belonging to 44 genera and 30 angiosperm families were recorded from the study area. About 61% of the vines were twiners, while other climbers and scramblers were represented by 24% and 9% respectively. Species richness and density of vines was lower in monsoon forests (MOIS) compared to the moisture-rich rainforests (Table 1). Species richness was maximum in SEMI (36 species) and minimum in MONT (Figure 1). Root climbers, mostly members of Araceae and Piperaceae, were abundant in SEMI and EVER. Species of *Calamus* with grapnel-like climbing mechanism were almost restricted to the rainforests. Smaller vines occur in both monsoon forests (e.g. *Asparagus racemosus*, *Dalbergia volubilis*) and rainforests (e.g. *Pothos scandens*, *Smilax zeylanica*). In MOIS, vine richness was less (9 species) and most of them were restricted to river banks or other moist areas.

Species–individual accumulation curve (individual-based rarefaction) against equal-sized sampling areas in different vegetation types showed a distinct difference in the richness and abundance. Steeper rarefaction curves indicate high heterogeneity. SEMI and EVER have the highest curves, which means that species diversity was

maximum in these vegetation types. Vegetation types with low species richness were SAVA and MONT (Figure 2). The overall difference in species richness among six vegetation types was statistically significant ($F_{5,179} = 65.1$, $P < 0.0001$). Species richness and the corresponding abundance showed significant positive correlation in all the vegetation types ($r = 0.84$–0.98, $P < 0.001$).

Tree density had a major influence on the density of vines. Density of trees was less in monsoon forests compared to the rainforests (Figure 3). In the rainforests, especially SEMI and EVER, tree strata are three-storied, consisting of small (5–15 m high), medium (16–32 m) and high (33–45 m) elements. Large-sized vines were quite abundant (density) in SEMI (53 individuals ha⁻¹) and less abundant in SUBT (14 individuals ha⁻¹). Density of mature trees was highest in MONT (853 individuals ha⁻¹) where vine density was negligible (Figure 4). There was significant difference in the density of vines among different vegetation types ($P < 0.0001$, $F_{4,54} = 49.8$). Density of tree saplings was highest (418 individuals ha⁻¹) in EVER (Figure 4). In all vegetation types, small vines

were abundant compared to larger ones (Figure 5). There was positive correlation between density of tree saplings (trellises) and small vines ($r = 0.558$, $P = 0.250$). Also there was a positive correlation between species richness and density of vines ($r = 0.852$, $P < 0.031$). In MONT, vines were represented by only three species (*Calamus huegelianus*, *Rubus ellipticus* and *Rubus niveus*), which belonged to smaller gbh categories and there were no vines in GRAS. Owing to high species richness and abundance, vines in SEMI (Table 1) showed highest Shannon index (2.92) and lowest Simpson index (0.09). Basal area of vines was higher in EVER (0.79 m²/ha, Table 1) and there was no significant difference in basal area among the forest types.

Twiners were the most dominant vines in majority of the vegetation types. Root climbers and grapnel climbers were totally absent in MOIS. Vines were rare in both SAVA and MONT (Table 2). Out of the 59 vine species, 47 were light-demanding (e.g. *Acacia torta*, *Calycopteris floribunda*, *Mimosa diplotricha*, *Ziziphus oenoplia*) while 12 were shade-tolerant (e.g. *Calamus hookerianus*, *C. huegelianus*, *Piper argyrophyllum*, *Pothos scandens*). Light-demanding species were larger in size, which covered the canopy of lofty trees, while shade-tolerant vines
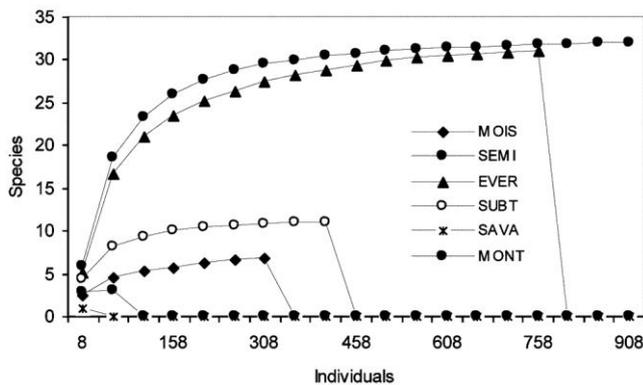

Figure 2. Individual-based rarefaction curves of different vegetation types. The curves were generated as a random series of 30 plots of 30 m × 30 m (i.e. 2.7 ha for each vegetation type). In the rarefaction curve, both SEMI and EVER seem to be quite similar in species richness, although EVER contained the highest number of individuals. Vegetation types like SAVA and MONT contain too few individuals to produce a comparable result.
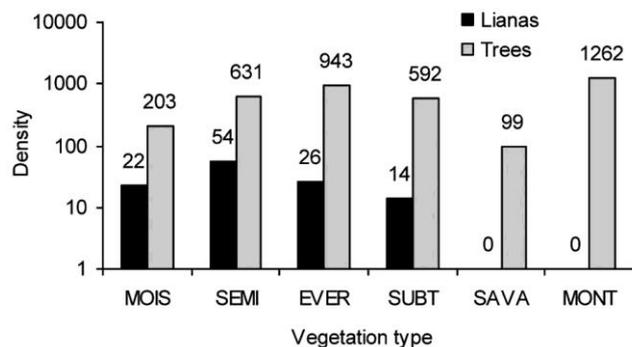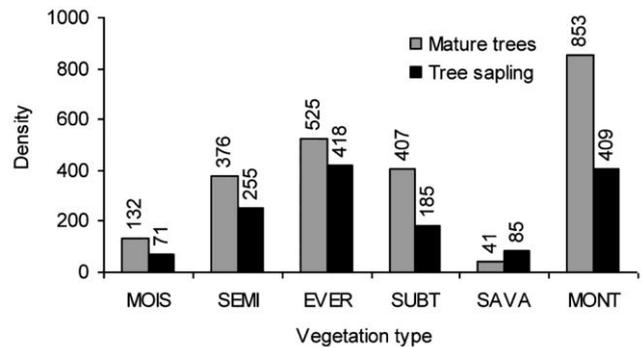

Figure 4. Comparison of density of mature trees (≥30 cm gbh) and tree saplings (10 ≥ 30 cm gbh) in different vegetation types. Proportion of tree saplings density was very high in EVER and SEMI.

Figure 3. A comparative analysis of the density of vines (>10 cm gbh) with that of trees (>10 cm gbh) showing negative correlation.
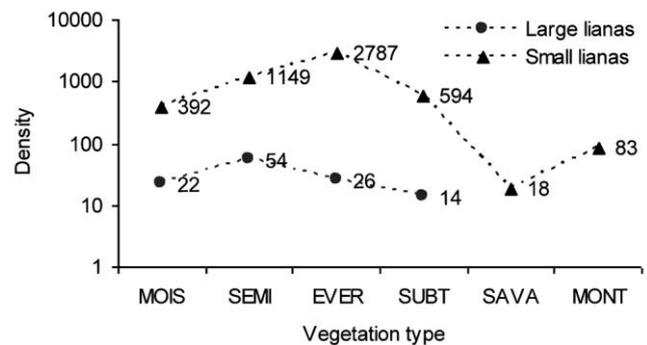

Figure 5. Differences in the density (in log scale) of large (≥10 and ≤30 cm gbh) and small vines (≥1 and <10 cm gbh) in different vegetation types. Both the types were abundant in SEMI and EVER and large vines were totally absent in SAVA and MONT.

Table 2. Species richness and abundance (in brackets) of vines under various climbing mechanisms distributed in different vegetation types

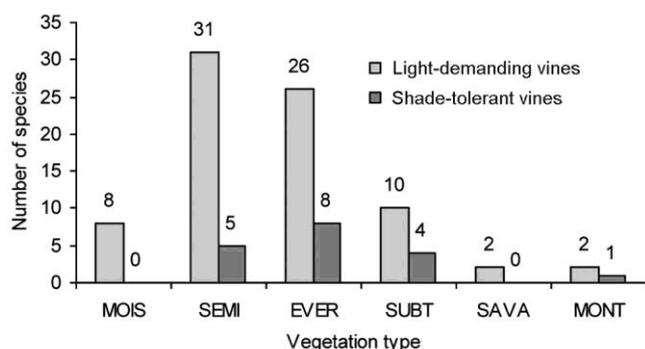| Climbing mechanism	Species richness and abundance in					
	MOIS	SEMI	EVER	SUBT	SAVA	MONT
Twiners	4 (287)	22 (553)	22 (546)	5 (157)	1 (1)	0
Scramblers	4 (21)	2 (12)	1 (17)	2 (13)	1 (12)	2 (52)
Root climbers	0	2 (62)	3 (37)	0	0	0
Hook climbers	1 (16)	7 (211)	3 (32)	3 (11)	0	0
Tendril climbers	1 (1)	3 (39)	2 (93)	2 (60)	0	0
Grapnel-like climbers	0	1 (95)	3 (110)	2 (200)	0	1 (37)

Figure 6. Proportion of light-demanding and shade-tolerant vines in different vegetation types of the study area.

were comparatively smaller (Figure 6). Most of the shade-tolerant species were monocots, and especially members of Arecaceae (e.g. *Calamus* spp., *Piper* spp., *Pothos scandens*).

Oligarchy and habitat preference

A total of 20 vine species, dominant across six vegetation types, accounted for 75% of all the individuals (Table 3). CV was used to predict the consistency of vine species occurrence within a forest type. In a particular site, species with both high dominance and low CV value reveal high predictability. In different vegetation types, the dominant species exhibited different distribution patterns. CV of vine density varied from 0.49 to 1.22 in the vine-rich vegetation type. In MOIS and SUBT, the top five dominant vines contributed 98% and 88% of the total density (Table 3). In SEMI and EVER, the top five species contributed 57% and 66% respectively, of density and scored a CV < 0.66 indicating moderate predictability of dominant species. But high CV value of MOIS (1.22) and EVER (1.09) indicates low predictability of dominant species, whereas low CV of SEMI (0.55) and SUBT (0.49) indicates high predictability of species. *Ventilago bombaiensis* was among the most dominant vine species, which showed high density in three vegetation types. Some of the species were highly abundant in a single vegetation type, but were not found elsewhere, e.g.

C. hookerianus in SUBT, *C. huegelianus* in MONT and *Ziziphus rugosa* in SAVA (Table 4). Dominant species were highly distributed in each vegetation type, but their frequency in other vegetation types was low. There was positive correlation between mean density of species and their corresponding frequency (% plots occupied) for vines ($r = 0.84–0.99$, $P < 0.0001$) among the different vegetation types.

Habitat preference of several vine species was also quite evident with 28 species (e.g. *Aganosma cymosa*, *C. hookerianus*, *Erycibe paniculata*) found only in one of the six vegetation types. Another set of 24 species (e.g. *Derris brevipes*, *Toddalia asiatica*, *V. bombaiensis*) was more generalist and shared three habitats. None of the vine species shared more than three habitats, which indicates their strong habitat specificity (Table 4, Figure 7). Most of the rare and endangered species (e.g. *C. huegelianus*, *C. pseudotenuis*) were restricted to single vegetation type.

Discussion

Species diversity

Species richness and abundance (density) of vines was higher in the medium elevation forests, especially SEMI and EVER, compared to the forests which occur in the foothills of the Ghats, i.e. MOIS. Richness of vines was high in SEMI, as it is a transitional zone between EVER and MOIS, composed of both evergreen and deciduous tree species, many of which shed their leaves during summer providing gap in the forest canopy for the flourishing of vines. So it is quite reasonable to infer that areas with high light conditions favour vine growth[11]. Also, in SEMI, the terrain has gentler slopes (5–20% slope) and many slow-flowing rivers and streams that improve the moisture content, which is congenial for the growth of vines. The use of species–individual curves provides a clear insight into species diversity. Rarefaction shows that species-rich communities like SEMI and EVER have less dominance than species-poor communities. Rarefaction curves predict the rate of accumulation of species with increasing number of individuals. The correlation

Table 3. Dominant species (first five) of vines and their distribution pattern in different vegetation types of the study area

Dominant vine species	Density of most dominant species in					
	MOIS	SEMI	EVER	SUBT	SAVA	MONT
Calycopteris floribunda	230	+	–	–	–	–
Dalbergia volubilis	56	–	–	–	–	–
Mimosa diplotricha	16	–	–	–	–	–
Acacia torta	16	–	–	–	–	–
Ziziphus rugosa	2	–	–	–	–	–
Ventilago bombaiensis	–	200	322	130	–	–
Acacia torta	+	142	+	–	–	–
Calamus thwaitesii	+	95	47	–	–	–
Thunbergia mysorensis	–	68	50	–	–	–
Anamirta cocculus	–	55	–	–	–	–
Smilax zeylanica	–	+	50	35	–	–
Cissus latifolia	–	+	43	–	–	–
Calamus hookerianus	–	–	–	128	–	–
Calamus pseudotenius	–	–	+	72	–	–
Passiflora subpeltata	–	–	–	25	–	–
Bridelia scandens	–	–	+	–	1	–
Ziziphus rugosa	+	+	–	–	12	–
Calamus huegelianus	–	–	–	–	–	37
Rubus niveus	–	–	–	–	–	27
Rubus ellipticus	–	–	–	–	–	25
Percentage of dominant vines	98	57	66	88	NA	NA
Coefficient of variation (CV)	122	55	109	49	–	–

'+' denotes presence of species; '–' indicates absence of corresponding species.
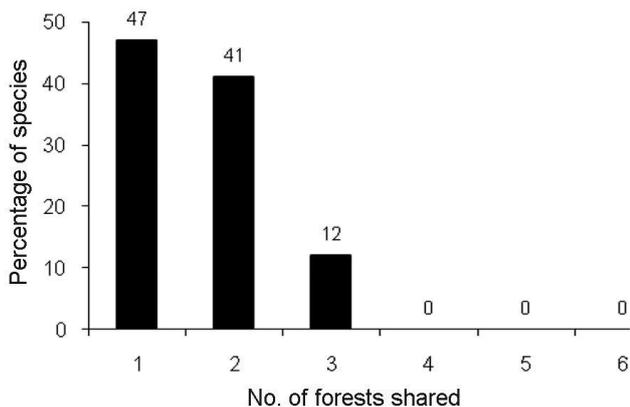

Figure 7. Habitat preference of vines. Percentage of taxa shared in different forest types indicates that most of the taxa adapted to one or two habitats and species distributed in more than three habitats are lacking.

between species richness and abundance suggests that the process affecting change in either richness or abundance also affects species diversity.

Majority of the vines are twiners which are distributed mostly in both high and low elevation forests due to their moisture and light requirements, while scramblers were restricted to MOIS and other disturbed habitats. In MOIS, rainfall is seasonal and hence soil moisture is lower. Therefore, richness and density of vines was lower, with most of them distributed in forest areas bordering rivers or streams. Longer dry season in the monsoon forests (MOIS) affects the survival and establishment rates of plants, which in turn decreases the number of potential coexisting functional types, and hence the number of vine species[45]. From fire-affected forest formations like SAVA with only a few trees, only two vine species were recorded. Obviously, the long and broad vessels occurring in the water-conducting systems of vines are sensitive to low water availability. Richness of vine species was strongly correlated with their density, even though their density was not related to water availability[34]. Water stress often causes embolism (air in the conducting vessels) in plants and frequent embolisms adversely affect their survival and growth. Hence in drought-prone areas the representation of vines is poor[46].

Density of trees in each of the vegetation types is negatively correlated with that of vines because of the compact canopy structure which restricts the penetration of light. Vine density is highest in SEMI due to a large number of twiners. In the vegetation types at higher elevations, viz. SUBT and MONT, tree density is very high and therefore, the tree canopy is more closed, rendering them unsuitable for the growth of vines. Also, temperature is very low and most of the vines are susceptible to low temperatures. This is because of the long and broad vessel elements of the vines coupled with their relatively narrow, uninsulated stems, which make them particularly

Table 4. Vines in various vegetation types of the study area

Species	MOIS	SEMI	EVER	SUBT	SAVA	MONT	Family
Acacia torta (Roxb.) Craib	+	*	–	–	–	–	Fabaceae
Aganosma cymosa (Roxb.) G. Don	+	–	–	–	–	–	Apocynaceae
Allophylus cobbe (L.) Raeusch.	–	–	+	–	–	–	Sapindaceae
Anamirta cocculus (L.) Wight & Arn.	–	+	–	–	–	–	Menispermaceae
Ancistrocladus heyneanus Wall. ex J. Graham	–	+	+	+	–	–	Ancistrocladaceae
Artabotrys zeylanicus Hook. f. & Thomson	–	+	+	–	–	–	Annonaceae
Asclepias sp.	–	+	+	–	–	–	Asclepiadaceae
Asparagus racemosus Willd.	–	+	–	+	–	–	Liliaceae
Bridelia scandens (Roxb.) Willd.	–	–	+	–	+	–	Euphorbiaceae
Caesalpinia cucullata Roxb.	–	+	–	–	–	–	Fabaceae
Caesalpinia mimosoides Lam.	+	–	–	–	–	–	Fabaceae
Caesalpinia spicata Dalzell	–	+	–	–	–	–	Fabaceae
Calamus hookerianus Becc.	–	–	–	*	–	–	Arecaceae
Calamus huegelianus Mart.	–	–	–	–	–	*	Arecaceae
Calamus metzianus Schltdl.	–	–	+	–	–	–	Arecaceae
Calamus pseudotenuis Becc.	–	–	+	+	–	–	Arecaceae
Calamus thwaitesii Becc.	–	+	+	–	–	–	Arecaceae
Calycopteris floribunda (Roxb.) Lam. ex Poir.	*	+	–	–	–	–	Combretaceae
Celastrus paniculatus Willd.	–	+	+	–	–	–	Celastraceae
Cissus latifolia Lam.	–	+	+	–	–	–	Vitaceae
Cissus repens Lam.	+	+	–	–	–	–	Vitaceae
Combretum latifolium Blume	–	+	+	–	–	–	Combretaceae
Croton laccifer L.	–	+	–	–	–	–	Euphorbiaceae
Cryptolepis buchananii Roem. & Schult.	–	+	–	–	–	–	Asclepiadaceae
Dalbergia horrida (Dennst.) Mabb.	+	+	–	–	–	–	Fabaceae
Dalbergia volubilis Roxb.	+	–	–	–	–	–	Fabaceae
Derris brevipes (Benth.) Baker	–	+	+	+	–	–	Fabaceae
Derris scandens (Roxb.) Benth.	–	–	+	–	–	–	Fabaceae
Diploclisia glaucescens (Blume) Diels	–	+	+	–	–	–	Menispermaceae
Embelia ribes Burm. f.	–	+	+	+	–	–	Myrsinaceae
Entada rheedii Spreng.	–	+	–	–	–	–	Fabaceae
Erycibe paniculata Roxb.	–	+	–	–	–	–	Convolvulaceae
Erythropalum scandens Blume	–	+	+	–	–	–	Erytropalaceae
Gnetum ula Brongn.	–	–	+	–	–	–	Gnetaceae
Hiptage benghalensis (L.) Kurz	–	–	+	–	–	–	Malpighiaceae
Jasminum rottlerianum Wall. ex DC.	–	+	+	–	–	–	Oleaceae
Mimosa diplotricha Sauvalle	+	–	–	–	–	–	Fabaceae
Myxopyrum smilacifolium (Wall.) Blume	–	–	+	–	–	–	Oleaceae
Passiflora subpeltata Ortega	–	–	–	+	–	–	Passifloraceae
Piper argyrophyllum Miq.	–	+	–	–	–	–	Piperaceae
Piper nigrum L.	–	+	+	–	–	–	Piperaceae
Pothos scandens L.	–	–	+	–	–	–	Araceae
Quisqualis malabarica Bedd.	–	+	+	–	–	–	Combretaceae
Rubus ellipticus Sm.	–	–	–	+	–	+	Rosaceae
Rubus niveus Thunb.	–	–	–	–	–	+	Rosaceae
Rubus rugosus Sm.	–	–	–	+	–	–	Rosaceae
Salacia fruticosa Wall.	–	+	+	–	–	–	Hippocratiaceae
Salacia oblonga Wall. *ex* Wight & Arn.	–	+	+	+	–	–	Hippocratiaceae
Sarcostigma kleinii Wight & Arn.	–	–	+	–	–	–	Icacinaceae
Smilax zeylanica L.	–	+	+	+	–	–	Smilacaceae
Strychnos colubrina L.	–	+	+	–	–	–	Loganiaceae
Tetrastigma leucostaphylum (Dennst.) Balakrishnan	–	–	+	+	–	–	Vitaceae
Tetrastigma sulcatum (Lawson) Gamble	–	+	+	–	–	–	Vitaceae
Thunbergia mysorensis (Wight) T. Anderson	–	+	+	–	–	–	Acanthaceae
Tiliacora acuminata (Lam.) Miers	–	+	+	–	–	–	Menispermaceae
Toddalia asiatica (L.) Lam.	–	+	+	+	–	–	Rutaceae
Ventilago bombaiensis Dalzell	–	+	*	+	–	–	Rhamnaceae
Ziziphus oenoplia (L.) Mill.	+	–	–	–	–	–	Rhamnaceae
Ziziphus rugosa Lam.	–	–	–	–	*	–	Rhamnaceae
Total species	9	36	34	14	2	3	Grand total: 59 species

'+' denotes presence of species; '–' indicates absence of corresponding species; '*' denotes dominant species represented in various vegetation types of the study area.

susceptible to freezing, causing irreversible vascular damage[5].

Tree saplings, to some extent, are also important to the vine population as potential trellises. The number of vine individuals was correlated with the number of tree saplings, as they act as trellises. Vines were more abundant in SEMI and EVER, possibly because of the three-storied forest structure and also availability of trellises. This indicates that when the canopy is more open, which is probably the case in areas with more number of small trees, it becomes easy for the light- or trellises-friendly vine elements to become established there. The total basal area of vines in EVER is higher than other vegetation types, and this may be due to preclimax nature of the vegetation type. Both SEMI and EVER have high amount of litter compared to high-elevation rainforests, where the steep slope (40–70%) of the terrain causes loss of the dry biomass during run-off[47]. Slope of the terrain has a direct effect on water availability by regulating run-off[48] and also leaching of soil nutrients. Loss of dry biomass due to run-off reduces soil fertility as well as water-holding capacity of the soil, and vine density and basal area may be less in such areas compared to fertile soils[1,49].

In the present study, it was found that vines were growing profusely in vegetation types with sufficient rainfall, low level of tree density and optimum temperature. Compared to MOIS, rainfall-rich forest types like SEMI and EVER have high abundance of vines. In MOIS, tree density is less and trees shed their leaves completely during summer. Therefore, all the vines in this vegetation type are light-demanding and shade-tolerant types are totally absent. SEMI has both light-demanding and shade-tolerant species and the forest type has a large number of trellises (tree saplings) which support vines in their early stages of growth. About 81% of vines are light-demanding and the remaining taxa belong to the shade-tolerant group. Shade-tolerant vine species like *Calamus* and *Piper* can survive below the forest canopy, in diffuse sunlight, and these plants are absent in MOIS. Monocot vines whose root system is fibrous and shallow, prefer moist and shaded environment. Shade-tolerant vines were restricted to rainforests, while light-demanding vines were seen in both monsoon forests and rainforests. Light-demanding vines cause more damage to the tree flora compared to shade-tolerant vines which rarely reach the canopy and often reproduce in the understorey[9].

Even though it is not reasonable to compare data generated on vine richness elsewhere in the world due to the differences in plot size and gbh classification parameters, in the tropical seasonal rainforests of Amazonia Bolivia[50], it ranged from 38 to 50 species (≥ 2 cm dbh) in 1 ha plot. Putz[51] found 65 vines species (≥ 2 cm dbh) per ha in Barro Colorado Island, and in Panama, this was 24–48 species (≥1 cm dbh). In the Western Ghats region, tropical dry forests of Anamalais[17,40] and evergreen forests of Agumbe[52] recorded a richness of 15–24 vine species. To generalize, richness and abundance of vines is very high in areas with high rainfall, medium tree density with more canopy gap and optimum temperature.

Spatial distribution and oligarchy

The strong frequency–density relationship found here may reflect a low level of habitat heterogeneity. Also, the strong correlation between density and frequency of these plants in different vegetation types proves that spatial distribution of dominant species is wider than rare species at local scale. Distribution of dominant species of a particular vegetation type is restricted to two or three vegetation types, i.e. dominant species in different vegetation types are not generalists. In other words, none of the generalist species are dominant in any of the vegetation types, which indicates environmental determinism effect or niche effect of species distribution. Vine communities following oligarchy tend to be dominated by limited sets of species. Hence, oligarchic dominance is not a result of the process which acts dichotomously causing some species to be dominant and others to be rare, but rather a process which affects species abundance in a more continuous fashion. Areas dominated by predictable oligarchies may be small where environmental heterogeneity is high[21]. Oligarchy is due to differential shade-tolerant nature of plants[53] and recent evidences suggest that shade tolerance varies in a continuous fashion among trees of the Neotropics[54]. Oligarchy dominance of species in the present study supports Burnham's findings of strong oligarchy dominance among vines in Yasuni[55,56].

Restriction of majority of species to a single vegetation type could be explained by the environmental determinism hypothesis, which considers forests as a mosaic where plant species composition is determined by edaphic and other environmental characteristics[57]. This can be explained by the dispersal ability and ecological adaptation to environmental conditions of different species by the so-called mass effect hypothesis, which maintains that trees or vines disperse their seeds over long distances, and therefore, there could be more woody plants growing in habitats where they cannot maintain viable populations on a long-term basis[58].

Conclusion

Species richness and abundance of vines depend on density of supporting trees, rainfall, light, temperature and elevation. Richness and abundance of vines is higher in the rainforests compared to the monsoon forests of the region. The results support the oligarchy hypothesis with profound dominance of limited sets of species in different vegetation types. Majority of species are restricted to a single forest type, and this endorses the environmental determinism hypothesis. Such patterns of vine dispersal

in the study area agree with the view that local ecological determinism and dispersal-limited ecological drift are important factors affecting species distribution pattern in the tropical forests of the region.

Management implications

Vines represent a sizable component of the total plant communities in most of the tropical forests around the world. They play a key role in the forest ecosystem and proliferate in canopy gaps and the tree-tops. In canopy gaps they can be profuse, thereby controlling the size of forest gap and negatively affecting the regeneration of trees. Recent findings also suggest that vines contribute to the transpiration loss in tropical forests, particularly during the dry season. Further, large vines which completely cover the tree crowns can have strong negative impacts on light availability to tree species, affecting their growth. Consequently, many forest managers and ecologists recommend intensive management of vines by periodic and pre-harvest removals. Also, pre-harvest vine-cutting can reduce the amount of collateral tree damage by up to 50% and reduce post-harvest canopy gap sizes[59] as noted in Asian and Neotropical forests. As observed during the study, light-demanding vines have a well-developed shoot system, and therefore, cause more damage to tree flora compared to shade-tolerant vines. At the same time, such vines help animals like primates, smaller mammals and reptiles to dwell on lofty trees and provide habitat for epiphytic orchids, ferns, etc. which contribute to the overall species diversity of the ecosystems occurring in the region.

1. Gentry, A. H., The distribution and evolution of climbing plants. In *The Biology of Vines* (eds Putz, F. E. and Mooney, H. A.), Cambridge University Press, England, 1991, pp. 3–52.
2. Gianoli, E., Evolution of climbing habit promotes diversification in flowering plants. *Proc. R. Soc. B – Biol. Sci.*, 2004, **271**, 2011–2015.
3. Stevens, G. C., Lianas as structural parasites: the *Bursera simaruba* example. *Ecology*, 1987, **68**, 77–81.
4. Perez-Salicrup, D. R. and Barker, M. G., Effect of liana cutting on water potential and growth of adult *Senna multijuga* (caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia*, 2000, **124**, 469–475.
5. Schnitzer, S. A. and Bongers, A., The ecology of lianas and their role in forests. *Trends Ecol. Evol.*, 2002, **17**, 223–230.
6. Fisher, J. B. and Ewers, F. W., Structural responses to stem injury in vines. In *The Biology of Vines* (eds Putz, F. E. and Mooney, H. A.), Cambridge University Press, England, 1991, pp. 99–126.
7. Balfour, D. and Bond, W., Factors limiting climber distribution and abundance in a southern African forest. *J. Ecol.*, 1993, **6**, 93–99.
8. Hegarty, F. E., Leaf litter production by lianas and trees in a subtropical Australian rainforest. *J. Trop. Ecol.*, 1991, **7**, 201–214.
9. Putz, F. E., How trees avoid and shed lianas. *Biotropica*, 1984, **16**, 19–23.
10. Stanley, W. G., Liana–tree interactions in a second-growth forest stand in eastern Amazonia. *J. Trop. Resour. Inst.*, 1997, **16**, 15–17.

11. Schnitzer, S. A., Dalling, J. W. and Carson, W. P., The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J. Ecol.*, 2000, **88**, 655–666.
12. Schenck, H., Beitrage zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten 1. Beitrage zur Biologie der Lianen. In *Botanische Mittheilungen aus den Tropen 4* (ed. Schimper, A. F. W.), 1892, pp. 1–253.
13. Nabe-Nielsen, J., Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. *J. Trop. Ecol.*, 2001, **17**, 1–19.
14. Uhl, G., Buschbacher, R. and DeSilva, G. H. G., Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica*, 1997, **29**, 250–260.
15. Laurance, W. F. *et al.*, Rainforest fragmentation and the structure of Amazonian liana communities. *Ecology*, 2001, **82**, 105–116.
16. DeWalt, S. J. and Chave, J., Structure and biomass of four lowland neotropical forests. *Biotropica*, 1999, **36**, 7–19; Givnish, T. J., On the causes of gradients in tropical tree diversity. *J. Ecol.*, 2004, **87**, 193–210.
17. Parthasarathy, N., Muthuramkumar, S. and Reddy, M. S., Patterns of liana diversity in tropical evergreen forests of peninsular India. *For. Ecol. Manage.*, 2004, **190**, 15–31.
18. Schnitzer, S. A., A mechanistic explanation for global patterns of liana abundance and distribution. *Am. Nat.*, 2005, **166**, 262–276.
19. Clinebell II, R. R., Phillips, O. L., Gentry, A. H., Stark, N. and Zuuring, H., Prediction of neotropical trees and liana species richness from soil and climatic data. *Biodivers. Conserv.*, 1995, **4**, 56–90.
20. Wright, S. J., *Plant Diversity in Tropical Forests of the Far East*, Clarendon Press, Oxford, UK, 2002, 2nd edn.
21. Pitman, N. C. A. *et al.*, Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, 2001, **82**, 2101–2117.
22. Wright, S. J., Calderón, O., Hernández, A. and Paton, S., Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology*, 2004, **85**, 484–489.
23. Wright, S. J. and Calderón, O., Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.*, 2006, **9**, 35–44.
24. Allen, B. P., Sharitz, R. R. and Goebel, P. C., Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? *For. Ecol. Manage.*, 2007, **242**, 17–23.
25. Granados, J. and Körner, C., In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. *Global Change Biol.*, 2002, **8**, 1109–1117.
26. Mohan, J. E., Ziska, L. H., Schlesinger, W. H., Thomas, R. B., Sicher, R. C., George, K. and Clark, J. S., Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO_2. *Proc. Natl. Acad. Sci. USA*, 2006, **103**, 9086–9089.
27. Zotz, G., Cueni, N. and Körner, C., *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO_2. *Funct. Ecol.*, 2006, **20**, 763–769.
28. Phillips, O. L. and Gentry, A. H., Increasing turnover through time in tropical forests. *Science*, 1994, **263**, 954–958.
29. Malhi, Y. and Wright, J., Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos. Trans. R. Soc. London, Ser. B*, 2004, **359**, 311–329.
30. Wright, S. J., Hernández, A. and Condit, R., The bushmeat harvest alters seedling banks by favoring lianas, large seeds and seed dispersed by bats, birds, and wind. *Biotropica*, 2007, **39**, 363–371.
31. Phillips, O. L. and Miller, J. S., *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Dataset*, Missouri Botanical Garden Press, St Louis, MO, USA, 2002.
32. Putz, F. E., Liana biomass and leaf area of a 'Tierra Firme' forest in the Rio Negro Basin, Venezuela. *Biotropica*, 1983, **15**, 185–189.

33. Phillips, O. L., Vasquez-Martınez, R., Monteagudo-Mendoza, A., Baker, T. R. and Nunez, V. R., Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, 2005, **86**, 1250–1258.

34. van den Heijden, G. M. F. and Phillips, O. L., What controls liana success in Neotropical forests? *Glob. Ecol. Biogeogr.*, 2008, **17**, 372–383.

35. van den Heijden, G. M. F. and Phillips, O. L., Environmental effect on Neotropical liana species richness. *J. Biogeogr.*, 2009, **36**, 1561–1572.

36. Proctor, J., Anderson, J. M., Chai, P. and Vallack, H. W., Ecological studies in four lowland rainforests in Gunung Mulu National Park, Sarawak. 1. Forest Environment, structure and floristics. *J. Ecol.*, 1983, **71**, 237–260.

37. Putz, F. E. and Chai, P., Ecological studies of lianas in Lambir National Park, Sarawak. *J. Ecol.*, 1987, **75**, 523–531.

38. Campbell, E. J. F. and Newbery, D. C., Ecological relationships between lianas and trees in lowland rainforests in Sahah, East Malaysia. *J. Trop. Ecol.*, 1993, **9**, 469–490.

39. Muthuramkumar, S. and Parthasarathy, N., Alpha diversity of lianas in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Divers. Distributions*, 2000, **6**, 1–14.

40. Reddy, M. S. and Parthasarathy, N., Liana diversity and distribution in four tropical dry evergreens on the Coromandel coast of South India. *Biodivers. Conserv.*, 2003, **12**, 1609–1627.

41. Champion, H. G. and Seth, S. K., *A Revised Survey of the Forest Type of India*, Oxford & IBH, New Delhi, 1968.

42. Nair, K. K. N., Monsoon forest of southern and South-East Asia. In *Encyclopedia of Forest Science* (ed. Burley, J.), Elsevier Academic Press, Amsterdam, 2003, pp. 1752–1762.

43. Richards, P. W., *The Tropical Rain Forest: An Ecological Study*, Cambridge University Press, London, 1996, 2nd edn.

44. Magurran, A. E., *Ecological Diversity and its Measurement*, Croom Helm Ltd, London, 1988.

45. Kleidon, A. and Mooney, H. A., A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biol.*, 2000, **6**, 507–523.

46. Gartner, B. L., Bullock, S. H., Mooney, H. A., Brown, V. B. and Whitbeck, J. L., Water transport properties of vines and tree stems in a tropical deciduous forest. *Am. J. Bot.*, 1990, **77**, 742–749.

47. Sundarapandian, S. M. and Swamy, P. S., Fine root biomass distribution and productivity pattern under open and closed canopies of tropical forests ecosystems at Kodayar in Western Ghats, South India. *For. Ecol. Manage.*, 1996, 181–192.

48. Williams, J. and Buckhouse, J. C., Surface run-off plot design for use in watershed research. *J. Range Manage.*, 1991, **44**, 411–412.

49. Huston, M., Soil nutrients and tree species richness in Cost Rican forests. *J. Biogeogr.*, 1980, **7**, 147–157.

50. Perez-Salicrup, D. R. and Sork, V. L., Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica*, 2001, **33**, 34–47.

51. Putz, F. E., The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 1984, **65**, 1713–1724.

52. Padaki, A. and Parthasarathy, N., Abundance and distribution of lianas in tropical lowland evergreen forest of Agumbe, central Western Ghats, India. *Trop. Ecol.*, 2000, **41**, 143–154.

53. Svenning, J. C., Kinner, D. A., Stallard, R. F., Engelbrecht, B. M. and Wright, S. J., Ecological determinism in plant community structure across a tropical forest landcape. *Ecology*, 2004, **85**, 2526–2538.

54. Wright, S. J., Muller-Landau, H. C., Condit, R. and Hubbell, S. P., Gap-dependent recruitment, realized vital rates and size distribution of tropical trees. *Ecology*, 2003, **84**, 3174–3185.

55. Burnham, R. J., Dominance, diversity and distribution of lianas in Yasuní, Ecuador: who is on top? *J. Trop. Ecol.*, 2002, **18**, 845–864.

56. Burnham, R. J., Alpha and beta diversity of vines in Yasuní, Ecuador. *For. Ecol. Manage.*, 2004, **190**, 43–55.

57. John, R., Dalling, J. W. and Harms, K. E., Soil nutrients influence spatial distributions of tropical tree species. *Proc. Natl. Acad. Sci. USA*, 2007, **104**, 864–869.

58. Shmida, A. and Wilson, M. V., Biological determinants of species diversity. *J. Biogeogr.*, 1985, **12**, 1–20.

59. Vidal, E., Johns, J., Gerwing, I. J., Barreto, P. and Uhl, C., Vine management for reduced-impact logging in eastern Amazonia. *For. Ecol. Manage.*, 1997, **98**, 105–114.