

Liana species composition, dominance and host interactions in primary and secondary forests in Malaysia

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Abstract: Lianas feature prominently in tropical forest ecosystems and yet information on their species composition and dominance as well as the patterns of liana-host interactions is scanty. The present study determined liana species composition, dominance and host interactions in thirty 40 m × 40 m plots established in primary (15 plots) and secondary (15 plots) forests within the Penang National Park, Malaysia. Lianas of diameter ≥ 2 cm were enumerated together with their hosts (dbh ≥ 10 cm) in the plots. Differences in liana species composition between the two forest types were determined by non-metric multidimensional scaling (NMDS) analysis, analysis of similarity (ANOSIM), and similarity of percentages (SIMPER). The patterns of species co-occurrence and nestedness were determined, respectively, by using c-score and NODF (a nestedness metric based on overlap and decreasing fill). The various composition analyses (NMDS and ANOSIM) indicated that liana species composition differed significantly between the two forest types. Furthermore, SIMPER revealed that only five liana species accounted for the top 50 % of the variation in species composition between the forests. The dominance of some liana species differed with respect to the primary and secondary forests, resulting in distinct group of liana species forming the most dominant liana flora in each forest type. Liana species showed negative co-occurrence pattern in the primary forest while random co-occurrence pattern was observed in the secondary forest. The findings further indicated that there was no significant nestedness among liana communities in the two forest types.

Key words: C-score, dominance, liana species composition, null model, species co-occurrence.

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Introduction

Lianas are woody climbers that germinate in the soil but later climb trees to obtain sunlight from the canopy, and attain great stature (Swaine *et al.* 2005). They occur in many parts of the world but

they are particularly more diverse and abundant in the tropics (Addo-Fordjour *et al.* 2008; Bongers *et al.* 2005). Lianas can comprise as much as 38 and 45 % of woody plant species (Addo-Fordjour *et al.* 2008) and abundance (cf. Schnitzer *et al.* 2006), respectively, in tropical forests. They exert strong

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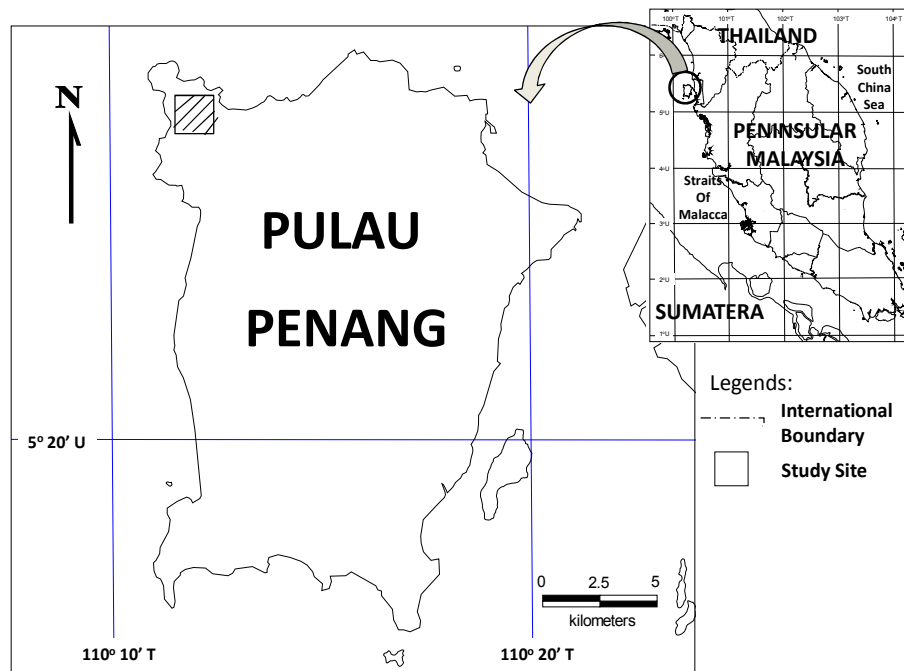


Fig. 1. Map of Penang State showing the Penang National Park, Malaysia.

ramifications in tropical forests in many ways (Schnitzer & Bongers 2011). Notably, lianas compete intensively with trees (Tobin *et al.* 2012) and hinder their natural regeneration processes (Schnitzer *et al.* 2005; Toledo-Aceves & Swaine 2008).

Several studies indicate that lianas are sensitive to human disturbance in tropical forests (e.g. Addo-Fordjour *et al.* 2012, 2013a; Mohandass *et al.* 2015; Schnitzer & Bongers 2011). Although many of the studies investigated the influence of human disturbance on liana assemblages, little is known about the patterns of liana species composition in relation to human disturbance. A recent study showed that even though liana species richness and basal area recovered after about six decades of human disturbance, liana species composition did not recover (Addo-Fordjour *et al.* 2016). This suggests that there is the need for species composition to be incorporated in liana assemblage studies in disturbed forests so as to fully understand how human disturbance affects liana assemblages. It has been reported that lianas are increasing in dominance in terms of abundance, basal area, biomass etc. within tropical forests (Schnitzer & Bongers 2011). Though many factors have been postulated to account for this trend, disturbance could be a major driver of

increasing liana dominance in tropical forests (see Schnitzer & Bongers 2011). At present, studies that examine the effects of human disturbance on liana species dominance are scarce. Studies conducted by Addo-Fordjour *et al.* (2013a, b) indicated that human disturbance influenced the patterns of liana species dominance in some tropical forests in Ghana.

Generally, there is less information about liana distribution in tropical forest ecosystems, but deeper analysis on how liana communities are structured is even more lacking. Understanding how interactions among species contribute to species distribution is central to community ecology (Lau *et al.* 2009). Species nestedness and co-occurrence analyses are among the major approaches used to determine plant assemblages in tropical forest ecosystems (Stone & Roberts 1990). These tools have received wide recognition and have been used extensively by community ecologists to evaluate whether communities are structured by random assemblages of species or by deterministic mechanisms such as competition for resources (Gotelli & McCabe 2002; Hausdorf & Hennig 2007). Although research works on lianas have gained momentum in the past decade, little is known about the patterns of liana-host interactions. Some works conducted in the area revealed

interesting and contrasting results (Blick & Burns 2009, 2011; Sfair *et al.* 2010). Sfair *et al.* (2010) observed a nested structure in liana-host interactions in three different neotropical forest vegetations. Nevertheless, Blick & Burns (2009) recorded no pattern in liana-host interactions in a temperate forest. Information on liana species co-occurrence and nestedness patterns may be useful in the management and conservation of forest ecosystems. This is particularly so in disturbed forests where environmental conditions can be inferred from the patterns generated (Mahecha *et al.* 2009). Since lianas depend on trees to gain access to the canopy, disturbances that affect trees and/or the lianas themselves may influence liana-host interactions in forest ecosystems. Consequently, the current study was conducted in a disturbed secondary forest and a primary forest so as to ascertain whether the patterns observed would be different between the two forest types.

The present study was carried out to investigate the effects of human disturbance on liana species composition and dominance within the Penang National Park, Malaysia. This study also determined the patterns of liana species co-occurrence and nestedness in primary and secondary forests in the national park. We addressed the following research questions: (1) does liana species composition differ between primary and disturbed secondary forests? (2) how does liana species dominance respond to human disturbance? and (3) what kind of species co-occurrence and nestedness patterns are exhibited by lianas in primary and secondary forests?

Methodology

Study area

The study was conducted in the Penang National Park, Penang, Malaysia (N 5° 27.583' E 100° 12.350') (Fig. 1) from September to October 2011. The national park which is said to be the smallest in the world has a total area of 1,213 ha. The national park consists of two forest types, primary and disturbed secondary forests. The park is reported to harbour over 1000 species of plants which are dominated by the families Dipterocarpaceae, Fabaceae, Apocynaceae, Anacardiaceae, Euphorbiaceae and Moraceae (Addo-Fordjour *et al.* 2012). The park is also rich in faunal diversity, with a total of 190 species, which includes 28 mammal, 14 reptile and 148 bird species, and other reptiles, insects and amphibians. The study

area became protected only in 2003 as a result of its conversion to a national park, and, therefore, it still shows signs of human disturbance in some parts of the forest. The secondary forest of the national park has undergone human disturbance such as logging, farming, hunting and gathering (Addo-Fordjour *et al.* 2012). Logging activities officially ended in 1996 but the other human activities continued till the area was designated as a national park in 2003. Currently, the secondary forest shows relics of considerable historical land uses such as clear cutting, farming, logging etc.

Sampling

In each forest type, lianas were sampled from three main sites namely, flatland, slope and valley, which were at least 5 km apart. Lianas were enumerated in five 40 m × 40 m plots, randomly demarcated in each site. Consequently, there were 15 plots sampled in each forest type, and 30 plots in the entire study area. Lianas of diameter ≥ 2 cm found on trees with diameter at breast height (dbh) ≥ 10 cm were identified and counted in each plot. Diameter of lianas was measured at a height of 1.3 m above ground level. Trees were also identified and counted in the plots. Plants were identified with the help of plant taxonomists, and also by the use of a manual and Floras (Dransfield 1979; Hooker 1875; Zhengyi *et al.* 2010). Voucher specimens were kept at the herbarium of the School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia.

Data analyses

Liana species composition and dominance

Liana species composition patterns in the primary and secondary forests were analysed using non-metric multidimensional scaling analysis (NMDS). Manhattan measure of dissimilarity was the distance measure used in this analysis. The dimension which yielded a lower stress was selected as the more suitable ordination dimension. Rare species can cause noise effect in NMDS analysis (Kennen 2005; Vonlanthen *et al.* 2006). Consequently, all rare liana species (species which were represented by < 5 stems and occurred in less than 10 % of the plots) were excluded from the NMDS analysis in order to minimise noise effect (Addo-Fordjour & Rahmad 2015; Kennen 2005; Vonlanthen *et al.* 2006). One-way analysis of similarity (ANOSIM) was used to test for significant difference in liana species composition of the

Table 1. Liana species dominance within the primary and secondary forests in the Penang National Park, Malaysia.

Species	Family	Importance value index	
		Primary forest	Secondary forest
<i>Agelaea borneensis</i> (Hook. f.) Merr.	Connaraceae	3.96	-
<i>Agelaea macrophylla</i> (Zoll.) Leenh.	Connaraceae	11.50	11.10
<i>Artabotrys maingayi</i> Hook. f. & Thomson	Annonaceae	1.44	-
<i>Artabotrys crassifolius</i> Hook. f. & Thomson	Annonaceae	44.80	9.76
<i>Bauhinia audax</i> (de Wit) G. Cusset	Fabaceae	1.43	-
<i>Bauhinia bidentata</i> Jack	Fabaceae	10.70	-
<i>Bauhinia ferruginea</i> Roxb	Fabaceae	8.96	3.04
<i>Bauhinia</i> sp.	Fabaceae	1.48	-
<i>Caesalpinia parviflora</i> (Prain ex King) Prain	Fabaceae	1.41	-
<i>Calamus longisetus</i> Thwaites	Palmae	2.23	-
<i>Calamus minutus</i> Dransf.	Palmae	-	2.41
<i>Calamus palustris</i> Griff.	Palmae	4.73	3.12
<i>Calamus tomentosus</i> Becc.	Palmae	-	2.37
<i>Cleghornia malaccensis</i> (Hook. f.) King & Gamble	Apocynaceae	1.49	-
<i>Cnestis palala</i> Merr.	Connaraceae	2.05	24.50
<i>Coptosapelta parviflora</i> Ridl.	Rubiaceae	10.30	14.50
<i>Cyathostemma hookeri</i> King	Annonaceae	3.25	6.44
<i>Daemonorops micracantha</i> (Griff.) Becc.	Palmae	2.75	-
<i>Dalbergia pinnata</i> (Lour.) Prain	Fabaceae	-	3.21
<i>Dalbergia rostrata</i> Hassk.	Fabaceae	36.30	3.65
<i>Dichapetalum longipetalum</i> (Turcz.) Engl.	Dichapetalaceae	-	4.43
<i>Ficus</i> sp.	Moraceae	2.56	-
<i>Fissistigma manubriatum</i> (Hook. f. & Thoms.) Merr.	Annonaceae	5.60	-
<i>Gnetum latifolium</i> Blume	Gnetaceae	20.80	5.75
<i>Gnetum</i> sp.	Gnetaceae	-	3.21
<i>Mitrella kentii</i> Miq.	Annonaceae	12.40	-
<i>Piper maingayi</i> Hook. f.	Piperaceae	5.42	-
<i>Porana spectabilis</i>	Convolvulaceae	-	4.12
<i>Rourea rugosa</i> Planch.	Connaraceae	3.46	5.59
<i>Salacia</i> sp.	Celastraceae	3.97	-
<i>Spatholobus ferrugineus</i> (Zoll. & Moritzi) Benth.	Apocynaceae	4.66	11.10
<i>Strophanthus perakensis</i> Scort. ex King & Gamble	Apocynaceae	1.44	3.00
<i>Strophanthus</i> sp.	Apocynaceae	1.48	-
<i>Strychnos axillaris</i> Colebr.	Loganiaceae	2.84	-
<i>Strychnos colubrina</i> L.	Loganiaceae	2.02	-
<i>Strychnos curtisii</i> King & Gamble	Loganiaceae	-	97.10
<i>Strychnos ignatii</i> Berg.	Loganiaceae	11.90	14.40
<i>Strychnos</i> sp.	Loganiaceae	3.52	-
<i>Tetracera indica</i> Merr.	Dilleniaceae	-	4.30
<i>Tetracera macrophylla</i> A. Chev.	Dilleniaceae	24.90	3.46
<i>Uncaria tomentosa</i> (Wild) D.C.	Rubiaceae	-	6.05
<i>Willughbeia angustifolia</i> (Miq.) Markgr.	Apocynaceae	30.00	19.70
<i>Willughbeia</i> sp.	Apocynaceae	12.90	22.30
<i>Ziziphus calophylla</i> Wall. ex Hook. f.	Rhamnaceae	-	9.01
<i>Ziziphus grewioides</i> (Warb.) L.M. Perry	Rhamnaceae	1.39	-
<i>Ziziphus</i> sp.	Rhamnaceae	-	2.65

two forest types. Thus, in a way, the ANOSIM provided a means of testing for significant difference in the composition patterns revealed in the NMDS analysis (Addo-Fordjour & Rahmad 2015; O’Dowd *et al.* 2003; Zoë 2010). Similarity percentage (SIMPER) analysis (using Bray-Curtis measure of similarity) was conducted to determine liana species that contributed to the top 50 % difference in liana species composition between the primary and secondary forests. All the above-mentioned analyses were conducted using the PAST programme (Hammer *et al.* 2001).

Liana species dominance was determined by the importance value index (IVI) of Cottam & Curtis (1956) expressed as follows: $IVI = RD + RF + RBA$

where, RD = relative density; RF = relative frequency; RBA = relative basal area

Liana species co-occurrence and nestedness patterns

To determine the co-occurrence patterns of liana species in each forest, community and liana guild matrices were analysed. Firstly, presence-absence matrices at the community level were generated for each forest to determine the pattern of co-occurrence. Each matrix consisted of rows, each of which was assigned a liana species, and columns, each of which represented a tree species. Liana species presence was denoted by 1 and its absence denoted as 0. Secondly, based on the vertical position of lianas recorded on the field, they were grouped into two categories namely, crown and trunk guilds according to Blick & Burns (2011). To determine whether species within each liana guild co-occur non-randomly, liana species (rows) in the community-level matrix of each forest was subdivided into crown and trunk guilds (Blick & Burns 2011). This resulted in two different compartments, each of which was made up of liana species found within the same regions of host species (Blick & Burns 2011). The c-score was used as the co-occurrence index due to its good power to detect non-random co-occurrence patterns in structured matrices that have noise (Gotelli 2000). The observed c-score was compared with 5000 simulation replicates generated using fixed-equiprobable null models. A significantly higher observed c-score in relation to the mean null model gave an indication of negative co-occurrence pattern. Additionally, nestedness analysis was performed to determine whether liana species assemblages on trees were nested by using NODF (a nestedness metric based on overlap and

decreasing fill). Abundance values of lianas were used in the nestedness matrices. The nestedness scores for NODF (WNODF) varies between 0 (complete disorder) and 100 (complete order). The significance of the observed metric values was determined from the 95 % confidence interval simulated after 5000 randomisations (Almeida-Neto & Ulrich 2011; Carvalho *et al.* 2011). Both the species co-occurrence and nestedness analyses were conducted using NODF software.

Results

Liana species composition and dominance

A total of 35 liana species were identified in the primary forest and 27 species of lianas were enumerated in the secondary forest (Table 1). A two-dimensional ordination provided a lower stress of 0.21, and was, therefore, chosen as the appropriate NMDS ordination. The first and second axes of the NMDS ordination revealed distinct liana species composition in the primary and secondary forests (Fig. 2). The plots in the primary forests were separated from those in the secondary forest to a great extent. This pattern was confirmed by the results of the one-way ANOSIM which indicated that liana species composition was significantly different between the two forest types ($r = 0.48$; $P = 0.0001$). Similarly, SIMPER analysis revealed considerable difference in liana species composition between the primary and secondary forests. The overall average dissimilarity in liana species composition between the forests was 91 %. The SIMPER analysis revealed that only five liana species accounted for the top 50 % of the species composition dissimilarity observed between the forests (Table 2).

Table 2. The most important species contributing to the top 50 % dissimilarity in liana species composition between the primary and secondary forests in the Penang National Park, Malaysia (Av. Dis. = Average dissimilarity, % contri. = Percentage contribution, % cum. contr. = Percentage cumulative contribution).

Species	Av. Dis.	% contri.	% cum. contr.
<i>Strychnos curtisii</i>	18.2	20.0	20.0
<i>Artabotrys crassifolius</i>	10.3	11.3	31.3
<i>Willughbeia</i> sp.	6.59	7.20	38.5
<i>Willughbeia angustifolia</i>	6.02	6.60	45.1
<i>Tetracera macrophylla</i>	5.83	6.40	51.5

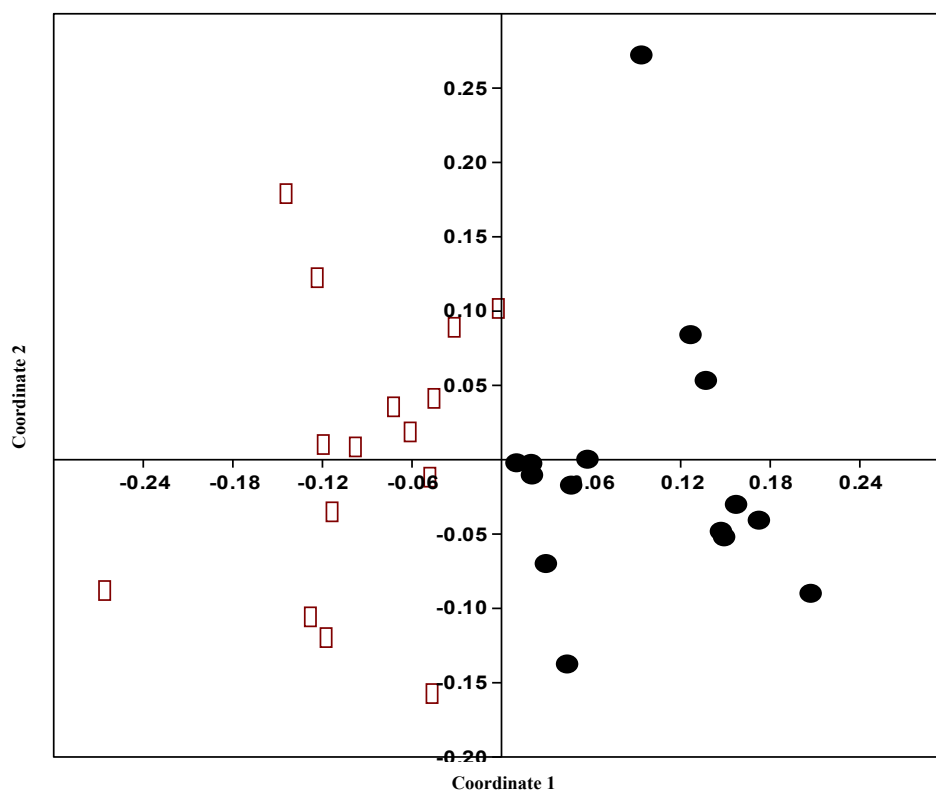


Fig. 2. Non-metric multidimensional scaling (NMDS) of liana species composition in the sampling plots of the primary (rectangles) and secondary (circles) forests in the Penang National Park, Malaysia.

Table 3. Co-occurrence patterns of liana species in primary and secondary forests.

Forest type	Observed C-score	Mean of expected C-score	<i>P</i> -value
Primary forest			
Community level	26.10	24.80	0.002
Trunk guild	6.13	6.19	0.341
Crown guild	12.30	12.10	0.129
Secondary forest			
Community level	17.10	17.00	0.413
Trunk guild	6.31	6.46	0.258
Crown guild	7.12	6.94	0.129

All *P* values are for "observed > expected".

Liana dominance was mainly restricted to one forest or the other (Table 1). Only *Willughbeia angustifolia* recorded high IVI in both forests. The most dominant liana species in the primary forest were *Artabotrys crassifolius* (IVI = 44.8), *Dalbergia rostrata* (IVI = 36.3), *Willughbeia angustifolia* (IVI = 30.0), *Tetracera macrophylla* (IVI = 24.9) and *Gnetum latifolium* (IVI = 20.8). In the secondary forest, *Strychnos curtisii* (IVI = 97.1), *Cnestis palala* (IVI = 24.5), *Willughbeia* sp. (IVI = 22.3) and *W. angustifolia* (19.7) were most dominant. Some species such as *A. crassifolius*, *D. rostrata*, *T.*

macrophylla, *G. latifolium* and *W. angustifolia* recorded considerably higher IVI in the primary forest than in the secondary forest. Likewise, certain species including *S. curtisii*, *C. palala* and *Willughbeia* sp. had higher IVI in the secondary forest compared to the primary forest.

Liana species co-occurrence and nestedness patterns

In the primary forest the observed c-score for liana species (community matrix) was significantly

higher than the mean null model expectation (Table 3; $P < 0.05$). However, the observed c-score for liana species in the secondary forest did not differ significantly from the null model communities ($P > 0.05$). Liana guild compartments produced the same result for both forests. In all cases, the observed c-score of the compartments was consistent with the mean null model expectation (Table 3; $P > 0.05$). The observed values of the nestedness metrics did not differ significantly from the null model in both forests (Table 4; $P = 0.05$).

Table 4. Summary of nestedness analysis of liana species in primary and secondary forests.

Forest	Observed	z-score	95 % CI simulated	P-value
Primary forest	6.21	-1.62	6.13-11.91	0.061
Secondary forest	5.77	-1.61	5.42-10.42	0.057

Discussion

The study revealed that there was significant variation in liana species composition between the primary and secondary forests in the Penang National Park, Malaysia. This pattern strongly provides support for a previous study which reported that liana species composition in some secondary forests varied considerably from the composition in primary forests (Yuan *et al.* 2009). The compositional difference between the primary and secondary forests can partly be attributed to human disturbance in the secondary forest. Liana cutting or harvesting was one of the key features of human disturbance in the secondary forest. This activity is capable of causing mortality and elimination of many liana species in disturbed areas although resistant species can survive and resprout vividly (Parren & Bongers 2001). This phenomenon most likely contributed to a shift in species composition in the secondary forest. It is interesting to note that even after 15 years of human disturbance, liana species composition in the secondary forest was still significantly different from that in the primary forest. This suggests that liana species composition recovery in disturbed forests could take many years to occur (Addo-Fordjour *et al.* 2016). Most of the liana species that dominated the primary forest exhibited low dominance in the secondary forest

and vice versa. This suggests that the dominance of different liana species most likely responded differently to human disturbance in the forest. The study indicated that some of the liana species maintained high dominance in the secondary forest, suggesting that disturbance probably enhanced the assemblage of those species in the secondary forest. One of such species was *S. curtisii*, which constituted about one-third of the total IVI in the secondary forest. The above-mentioned trend is consistent with some previous works which reported that human disturbance influenced liana species dominance in some tropical forests (Addo-Fordjour *et al.* 2013a, b).

The significantly higher observed c-score in relation to the mean null model expectation in the primary forest is an indication of negative co-occurrence pattern of interaction among the species. This pattern of species segregation may be due to competition by liana species for limited resources in the primary forest. Sunlight is an important resource for liana proliferation and development in tropical forests (Madeira *et al.* 2009). However, sunlight is usually a limited resource in primary forests due to high canopy cover. Consequently, competition for sunlight by lianas in the primary forest could result in a distribution pattern in which the common occurrence of liana species were reduced or avoided (Tello *et al.* 2008). It must be added that competition for other resources such as soil physico-chemical factors might have also played an important role in influencing liana species assemblages in the primary forest. Whatever be the case, probable competition among liana species in the primary forest could result in a reduction in overlap between the species (Genini *et al.* 2012). Host specificity by lianas, and matching micro-habitat preferences between lianas and their hosts could have also been responsible for the negative co-occurrence patterns (Blick & Burns 2009).

Abundance of resources in a habitat can cause species to show random co-occurrence patterns since competition between the species is reduced or avoided (Tiho & Josens 2007). This explanation may underlie the random co-occurrence pattern of liana species observed in the secondary forest. In the presence of abundant sunlight in the secondary forest, competition among the species might have been less or avoided. The presence of random co-occurrence pattern of liana species in the secondary forest suggests a possible disruption of liana host specificity by human disturbance. The two liana guilds, trunk and crown, produced the same results (random co-occurrence pattern) indicating that

human disturbance did not have much influence on the distribution of liana species within each guild. A similar result was found in the work of Blick & Burns (2011) in which liana species in trunk and crown guilds were each randomly distributed.

The findings on nestedness analysis indicated that there was no significant structure in the liana-host interactions. This demonstrates that although liana species in the primary forest exhibited negative co-occurrence, there was no structure in the species segregation. The absence of nestedness in the two forest types may be due to differential ability of liana species to colonise trees and/or trees to avoid lianas, and the presence of heterogeneous composition of host species in the forests (Genini *et al.* 2012).

Conclusions

Human disturbance influenced liana species composition to a great extent, and the difference in liana species composition between the primary and secondary forests was significant. Dominance of some liana species differed between the primary and secondary forests. Liana species in the primary forest exhibited negative co-occurrence pattern while those in the secondary forest showed random co-occurrence pattern. The findings also revealed that there was no significant nested structure in liana-host interactions in the two forest types.

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References

- Addo-Fordjour, P., A. K. Anning, E. A. Atakora & P. S. Agyei. 2008. Diversity and distribution of climbing plants in a semi-deciduous rain forest, KNUST Botanic Garden, Ghana. *International Journal of Botany* **4**: 186-195.
- Addo-Fordjour, P., Z. B. Rahmad & A. M. S. Shahrul. 2012. Effects of human disturbance on liana community diversity and structure in a tropical rainforest, Malaysia: implication for conservation. *Journal of Plant Ecology* **5**: 391-399.
- Addo-Fordjour, P., Z. B. Rahmad, J. Amui, C. Pinto & M. Dwomoh. 2013a. Patterns of liana community diversity and structure in a tropical rainforest reserve, Ghana: effects of human disturbance. *African Journal of Ecology* **51**: 217-227.
- Addo-Fordjour, P., P. El Duah & D. K. K. Agbesi. 2013b. Factors influencing liana species richness and structure following anthropogenic disturbance in a tropical forest, Ghana. *ISRN Forestry* Vol. 2013, Article ID 920370, 11 pages, doi:10.1155/2013/920370.
- Addo-Fordjour, P. & Z. B. Rahmad. 2015. Environmental factors associated with liana community assemblages in a tropical forest reserve, Ghana. *Journal of Tropical Ecology* **31**: 69-79.
- Addo-Fordjour, P., Z. B. Rahmad, A. M. S. Shahrul & M. Asyraf. 2016. Impacts of forest management on liana diversity and community structure in a tropical forest in Ghana: implications for conservation. *Journal of Forestry Research* **27**: 147-153.
- Almeida-Neto, M. & W. Ulrich. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software* **26**: 173-178.
- Blick, R. A. J. & K. C. Burns. 2009. Network properties of arboreal plants: Are epiphytes, mistletoes and lianas structured similarly? *Perspectives in Plant Ecology, Evolution and Systematics* **11**: 41-52.
- Blick, R. A. J. & K. C. Burns. 2011. Liana co-occurrence patterns in a temperate forest. *Journal of Vegetation Science* **22**: 868-877.
- Bongers, F., M. P. E. Parren, M. D. Swaine & D. Traoré. 2005. Forest climbing plants of West Africa: introduction. pp. 5-18. In: F. Bongers, M. P. E. Parren & D. Traoré (eds.) *Forest Climbing Plants of West Africa: Diversity, Ecology and Management*. CAB International, Wallingford, Oxfordshire, UK.
- Carvalho, J. C., P. Cardoso & P. Gomes. 2011. Determining the relative roles of species replacement and species richness differences in generating beta diversity patterns. *Global Ecology and Biogeography* **21**: 760-771.
- Cottam, G. & J. T. Curtis. 1956. The use of distance measurement in phytosociological sampling. *Ecology* **37**: 451-460.
- Dransfield, J. 1979. *A Manual of the Rattans of the Malay Peninsula*. Malaysian Forest Records. Number 29. Forest Department, Ministry of Primary Industries.

- Genini, J., M. C. Côrtes, P. R. Guimarães & M. Galetti. 2012. Mistletoes play different roles in a modular host-parasite network. *Biotropica* **44**: 171-178.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* **81**: 2606-2621.
- Gotelli, N. J. & D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* **83**: 2091-2096.
- Hammer, Ø., D. A. T. Harper & P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**: 9.
- Hausdorf, B. & C. Hennig. 2007. Null model testes of clustering of species, negative co-occurrence patterns and nestedness in metacommunities. *Oikos* **116**: 818-828.
- Hooker, J. D. 1875. (Assisted by various botanists). *The Flora of British India*. Volume 1. University of California Libraries, L. Reeve & Co. Ltd., Kent, England. Indian Reprint 1973. Bishen Singh Mahendra Pal Singh, Dehra Dun. India.
- Kennen, J. G. 2005. Effects of landscape change on fish assemblage structure in a rapidly growing metropolitan area in North Carolina, USA. *American Fisheries Society Symposium* **47**: 39-52.
- Lau, M. K., L. E. Hagenauer & T. G. Whitham. 2009. Assemblage-structuring force of species interactions varies spatially and temporally: Co-occurrence analysis of canopy arthropod distributions. Ecological Society of America (ESA) Meeting, Albuquerque, NM. Available from Nature Precedings <<http://dx.doi.org/10.1038/npre.2009.3600.1>>.
- Lindo, Z. 2010. Communities of Oribatida associated with litter input in western red cedar tree crowns: are moss mats 'magic carpets' for oribatid mite dispersal? pp. 143-148. In: M. W. Sabelis & J. Bruin (eds.) *Trends in Acarology: Proceedings of the 12th International Congress of Acarology*. Dordrecht: Springer.
- Madeira, B. G., M. M. Espírito-Santo, S. D. Neto, Y. Nunes, G. A. Sánchez Azofeifa, G. W. Fernandes & M. Quesada. 2009. Changes in tree and liana communities along successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology* **201**: 291-304.
- Mahecha, M. D., A. Martínez, H. Lange, M. Reichstein & E. Beck. 2009. Identification of characteristic plant co-occurrences in neotropical secondary montane forests. *Journal of Plant Ecology* **2**: 31-41.
- Mohandass, D., P. Davidar, S. Somasundaram, L. Vijayan & K. C. Beng. 2015. Influence of disturbance regime on liana species composition, density and basal area in the tropical montane evergreen forests (sholas) of the Western Ghats, India. *Tropical Ecology* **56**: 169-182.
- O'Dowd, D. J., P. T. Green & P. S. Lake. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* **6**: 812-817.
- Parren, M. P. E. & F. Bongers 2001. Does climber cutting reduce felling damage in southern Cameroon? *Forest Ecology and Management* **141**: 175-188.
- Schnitzer, S. A., M. Kuzee & F. Bongers. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* **93**: 1115-1125.
- Schnitzer, S. A., S. J. DeWalt & J. Chave. 2006. Censusing and measuring lianas: A quantitative comparison of the common methods. *Biotropica* **38**: 581-591.
- Schnitzer, S. A. & F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* **14**: 397-406.
- Sfair, J. C., A. L. C. Rochelle, A. A. Rezende, J. Van Melisb, V. L. Weiser & F. R. Martins. 2010. Nested liana-tree network in three distinct neotropical vegetation formations. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 277-281.
- Stone, L. & A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* **85**: 74-79.
- Swaine, M. D., W. D. Hawthorne, F. Bongers & M. Toldedo-Aceves. 2005. Climbing plants in Ghanaian forests. pp. 93-107. In: F. Bongers, M. P. E. Parren & D. Traoré (eds.) *Forest Climbing Plants of West Africa: Diversity, Ecology and Management*. CAB International, Wallingford, Oxfordshire, UK.
- Tello, J. S., R. D. Stevens & C. W. Dick. 2008. Patterns of species co-occurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. *Oikos* **117**: 693-702.
- Tiho, S. & G. Josens. 2007. Co-occurrence of earthworms in urban surroundings: A null model analysis of community structure. *European Journal of Soil Biology* **43**: 84-90.
- Tobin, M. F., A. J. Wright, S. A. Mangan & S. A. Schnitzer. 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere* **3**: 1-11.
- Toledo-Aceves, T. & M. D. Swaine. 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecology* **196**: 233-244.
- Vonlanthen, C. M., A. Bühler, H. Veit, P. M. Kammer & W. Eugster. 2006. Alpine plant communities: a

statistical assessment of their relation to micro-climatological, pedological, geomorphological, and other factors. *Physical Geography* **27**: 137-154.

Yuan, C., W. Liu, C. Q. Tang & X. Li. 2009. Species composition, diversity, and abundance of lianas in different secondary and primary forests in a sub-

tropical mountainous area, SW China. *Ecological Research* **24**: 1361-1370.

Zhengyi, W., P. H. Raven & H. Deyuan. 2010. *Flora of China*. Volume 10: Fabaceae. Missouri Botanical Garden Press.

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