Edge disturbance shapes liana diversity and abundance but not liana-tree interaction network patterns in moist semi-deciduous forests, Ghana

Bismark Ofosu-Bamfo[1], Patrick Addo-Fordjour[2], and Ebenezer Belford[2]

[1]University of Energy and Natural Resources, Sunyani, Ghana
[2]Kwame Nkrumah University of Science and Technology

May 25, 2021

Abstract

We evaluated the response of liana community structure and the patterns of liana-tree interaction structure to forest edge in two moist semi-deciduous forests in Ghana (Asenanyo and Suhuma Forest Reserves: AFR and SFR, respectively). Liana community structure and liana-tree interactions were assessed in 24 50 × 50 m randomly located plots in three forest sites in each forest: edge, interior and deep-interior established at 0-50 m, 200 m and 400 m from edge. Edge effects positively and negatively influenced liana diversity in forest edges of AFR and SFR, respectively. There was a positive influence of edge disturbance on liana abundance in both forests. More liana species experienced positive magnitude of edge influence (MEI) on their abundance. We observed anti-nested structure in all the liana-tree networks in AFR, while no nestedness was observed in the three networks in SFR. The networks in both forests were less connected, and more modular and specialised than their null models. Many liana and tree species were specialised, with the specialisation tending to be symmetrical. Topologically, most of the species were peripherals, with only a few connectors, module hubs, and network hubs. Some of the species showed consistency in their topological roles from one site to another, while the roles of other species changed. Generally, liana species co-occurred randomly on tree species in all the forest sites except edge site in the Asenanyo Forest Reserve. The findings of the study deepen our understanding of liana-tree interactions, provide implications for conservation, and may contribute to development of a robust edge theory.

Edge disturbance shapes liana diversity and abundance but not liana-tree interaction network patterns in moist semi-deciduous forests, Ghana

Running title:

Edge effects on lianas and liana-tree interactions

Bismark Ofosu-Bamfo[1], Patrick Addo-Fordjour[2*], E.J.D. Belford[2]

[1]Department of Basic and Applied Biology, School of Sciences, University of Energy and Natural Resources, Sunyani, Ghana

[2]Department of Theoretical and Applied Biology, Faculty of Biosciences, College of Science, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

*Corresponding author: paddykay77@yahoo.com; paddofordjour.cos@knust.edu.gh

ABSTRACT

We evaluated the response of liana community structure and the patterns of liana-tree interaction structure to forest edge in two moist semi-deciduous forests in Ghana (Asenanyo and Suhuma Forest Reserves: AFR and SFR, respectively). Liana community structure and liana-tree interactions were assessed in 24 50 × 50 m randomly located plots in three forest sites in each forest: edge, interior and deep-interior established at 0-50 m, 200 m and 400 m from edge. Edge effects positively and negatively influenced liana diversity in forest edges of AFR and SFR, respectively. There was a positive influence of edge disturbance on liana abundance in both forests. More liana species experienced positive magnitude of edge influence (MEI) on their abundance. We observed anti-nested structure in all the liana-tree networks in AFR, while no nestedness was observed in the three networks in SFR. The networks in both forests were less connected, and more modular and specialised than their null models. Many liana and tree species were specialised, with the specialisation tending to be symmetrical. Topologically, most of the species were peripherals, with only a few connectors, module hubs, and network hubs. Some of the species showed consistency in their topological roles from one site to another, while the roles of other species changed. Generally, liana species co-occurred randomly on tree species in all the forest sites except edge site in the Asenanyo Forest Reserve. The findings of the study deepen our understanding of liana-tree interactions, provide implications for conservation, and may contribute to development of a robust edge theory.

Keywords: co-occurrence patterns, ecological networks, edge influence, liana diversity and abundance, modularity, nestedness, specialisation

INTRODUCTION

In tropical forests, particularly in developing economies, human interactions with forest ecosystems remain an important source of change in their structure (FAO & UNEP, 2011) and functioning (Pedro et al., 2015). A common outcome of human interface with forest ecosystems is fragmentation which results in the creation of edges (Harper et al., 2005). Edge mediated microclimatic changes may favour disturbance-adapted, light-loving species such as lianas (see Hawthorne, 1996; Laurance et al., 2001), but generally be disadvantageous to others such as trees (Laurance et al., 2006). Previous studies reported that edge effects enhanced liana diversity and abundance in some forests (Laurance et al., 2001; Campbell et al., 2018; Ofosu-Bamfo et al., 2019), but others did not detect changes in liana diversity in response to edge (Mohandass et al., 2014; Ofofu-Bamfo et al., 2019). Several properties of forest edge such as edge size, edge type, and surrounding matrix type can mediate edge effects on plant community structure (Martino, 2015), and be responsible for the varied responses of community structure to edges in different forests. As liana community assemblages respond to edge disturbance, the relationship between lianas and trees may also be altered. Fagan et al. (1999) stated that habitat edges can modify species interactions. Similarly, Porensky (2011) reported that species interactions show strong responses to forest edge. Nonetheless, there is scarcity of information on the response of liana-tree interaction network patterns to forest edge.

The knowledge of liana-tree interactions and the factors that shape them are key to fully understanding plant community composition and structure. Although different patterns of liana-tree interactions have been reported in literature, there is no consensus yet. For example, nestedness, a network pattern in which the interactions of less connected species form proper subsets of the interactions of more connected species (Bascompte et al., 2003; Landi et al., 2018; Ponisio, et al. 2019), has been used to characterise the structure of liana-tree networks. Different patterns of nestedness are reported in literature including nested (Sfair et al., 2010) and non-nested (Addo-Fordjour & Afram, 2021; Addo-Fordjour et al., 2016; Blick & Burns, 2009; Magrach et al., 2015; Ofosu-Bamfo et al., 2019) structures. Among the studies that did not find nested structure in liana-tree netowrks, some reported anti-nested structure which depicts non-random assembly (Addo-Fordjour & Afram, 2021; Blick & Burns, 2009; Magrach et al., 2015), whiles others observed non-significant nestedness that shows random assembly (Addo-Fordjour et al., 2016; Ofosu-Bamfo et al., 2019). Ecological networks can also be compartmentalised into modules whose members interact more among themselves (Carstensen et al., 2016). This phenomenon referred to as modularity, is predicted to stabilise ecological networks (Massol et al., 2017; Thébault & Fontaine, 2010). For this reason, modularity analysis of liana-tree networks can have implications for forest management and conservation. Nonetheless, only a few studies assessed the patterns of modularity in liana-tree networks. Sfair et al. (2015) did not find modular structure in their networks, but Addo-Fordjour & Afram (2021) recorded significant modular structure in liana-tree networks.

Specialisation at the network and species levels can cause non-nested and modular organisation of species (Addo-Fordjour & Afram, 2021; Médoc et al., 2017; Castledine et al., 2020). Thus, in liana-tree networks in which coevolution leads to specialisation (Sfair et al., 2015), the networks may tend to be non-nested and/or modular. Another important metric used to characterise network structure is species co-occurrence, which describes the frequency of pairs of liana species to co-occur on the same phorophyte species (Zulqarnain et al., 2016). Like the above-mentioned network metrics, mixed patterns of liana species co-occurrence have been reported in literature, which include positive co-occurrence (Addo-Fordjour et al., 2016; Zulqarnain et al., 2016), negative co-occurrence (Blick & Burns, 2011, 2009), and random co-occurrence (Addo-Fordjour et al., 2016). With the mixed findings on the structure of liana-tree interactions in literature, there is the need for more studies to be conducted to determine the most consistent patterns. Knowledge of co-occurrence patterns is important for increasing our understanding of species interactions and predicting community stability and maintenance, and ecosystem functioning, all of which may be useful in forest conservation (Vizentin-Bugoni et al., 2016).

The current study determined the response of liana community assemblages and the patterns of structure of liana-tree interaction networks to edge in two moist semi-deciduous forests in Ghana. The forest edges we studied were surrounded by large matrices of crop farmlands, thus making the edges much exposed. The nature and size of land matrix bordering forest edges play a key role in determining the intensity of edge effects on plant community structure (Aragón et al., 2015). To this end, edges bordered by wide land matrices are expected to exert stronger effects on plant communities than edges surrounded by narrow area of land (Addo-Fordjour & Owusu-Boadi, 2016). Furthermore, because the nature of the land matrix surrounding our forest edges is physiognomically dissimilar to the forest vegetation, the microclimate variation between the forest edge and interior may be enhanced (Aragón et al., 2015). Thus, edge effects on lianas and liana-tree interaction patterns in the two moist semi-deciduous forests may be apparent. Edge disturbance permits greater penetration of sunlight into forest edges, and also increases forest edge dryness (Thier & Wesenberg, 2016), both of which can favour liana proliferation. On the basis of the above, we tested the following hypotheses:

1. Liana diversity and abundance would be higher in edge site than non-edge sites.
2. We expected that as edge disturbance enhances liana abundance at the forest edge, network connectance will increase, resulting in less specialised, nested, and non-modular network structures in edge site, while the networks in the non-edge sites will be less connected, more specialised, non-nested, and modular.
3. Edge effects will cause shifts in topological roles of liana and tree species due to changes in the distribution and abundance of the species.
4. As sunlight and dry conditions are elevated at edge sites relative to the non-edge sites, competition of lianas for the resources in edge site may be lower. Moreover, as edge effects tend to cause tree mortality at forest edges (Murcia 1995), the number of available host species may reduce, increasing liana infestation per host. Thus, we expected that liana species in edge sites would show positive co-occurrence on host trees, while the species in non-edge sites will randomly co-occur on their hosts.

The findings of our study would be useful in the management of forest edges and conservation of edge species. Our study seeks to add valuable information to literature, thus helping to obtain general patterns of liana assemblages and structure of liana-tree interactions in relation to edge effects. The findings would also contribute to the development of a robust edge theory in view of the fact that there is dearth of information on the role of edge disturbance in shaping the patterns of liana-tree network structure in forests.

METHODOLOGY

Study areas

We conducted the study in two moist semi-deciduous tropical forest ecosystems in Ghana: Asenanyo Forest Reserve (latitudes 6°17' and 6°36'N; longitudes 1°50' and 2°16'W) and Suhuma Forest Reserve (latitudes 5°56' and 6°11'N; longitudes 2°21' and 2°36'W).

Asenanyo Forest Reserve

The Asenanyo Forest Reserve is a production forest that was established in the year 1940 and covers an area of 22,800 ha in the Ashanti Region of Ghana (Wiafe, 2014). It is of the moist semi-deciduous forest ecosystem, with the dominant tree species being *Celtis mildbraedii* , *Triplochiton scleroxylon* , *Entandrophragma*spp. and *Thaumatococus* spp. (Wiafe, 2014; Forest Services Division, 2010a). The forest has a bimodal rainy season from April to October (maximum rainfall: May-June; minimum rainfall: September-October) and a dry season from November to March. Annual rainfall range is 1250–500 mm (Hall & Swaine, 1981). Temperature in the reserve ranges from an average high of 30.5°C to 21°C, with a mean annual relative humidity of about 84%. Asenanyo Forest Reserve has about 20 admitted farms scattered throughout the reserve, the size of each averaging approximately 5 ha (Forest Services Division, 2010a). The reserve also has one admitted community occupying an area of about 955.70 ha (Forest Services Division, 2010a). Threats faced by the reserve include illegal logging, charcoal production, illegal farming in the reserve, surface mining, sand wining and hunting (Wiafe, 2014; Forest Services Division, 2010a). These activities are accompanied by unauthorized development of in-roads and clearing of forest.

Suhuma Forest Reserve

The Suhuma Forest Reserve (latitudes 5°56' and 6°11'N; longitudes 2°21' and 2°36'W) is also a production forest of about 36,030 ha located in the Sefwi Wiawso Forest District (Hawthorne & Abu-Juan, 1995). There are 24 admitted farms in the reserve each averaging 11.5 ha (total 276 ha) and one admitted community covering an area of 389 ha (Forest Services Division, 2010b). The reserve is exposed to active logging. Its canopy is discontinuous due to excessive logging activity but still has emergent trees that may reach heights of about 40 m. Most of the trees that occur in the reserve are deciduous: (Forest Services Division, 2010b). The forest lies within the moist semi-deciduous forest zone in Ghana, and thus its vegetation is dominated by tree species such as*C . mildbraeddii* , *Baphia nitida* , *Nesogordonia papaverifera* , *Microdesmis puberula* , *Khaya ivoriensis* ,*Daniella ogea* , and *Dacryodes klaineana* (Hall & Swaine, 1981). The forest reserve experiences two distinct seasons: the dry season and the rainy season. The dry season is from December to March whereas April to October marks the rainy season. Average annual rainfall is between 1300 and 1600 mm. Mean annual temperature ranges between 26 and 29°C, and relative humidity is usually above 90 % in the rainy season and falls to 60% during the dry season (Forest Services Division, 2010b).

Sampling design and data collection

A total of eight 50 × 50 m plots were randomly established in each of three forest sites namely, edge, interior and deep-interior. Each forest site had two randomly demarcated and independent sampling areas, each of which contained four plots. The edge site was defined as 0-50 m from the forest edge, while interior and deep-interior sites were 200 m and 400 m from the forest edge, respectively. Variable penetration distances of edge have been reported in previous studies. A lot of studies revealed that edges can extend up to 100 m from the forest edge, while other studies also detected edge effects up to 300 m (see Ofosu-Bamfo et al., 2019). Thus, we set our two interior sites 100 m beyond each of the aforementioned edge penetration distance limit, resulting in 200 m and 400 m distances from the forest edge.

We surveyed and identified all lianas with diameter (at 1.30 m from the rooting base) [?] 1 cm as well as trees (diameter at breast height [?] 10 cm) that carried lianas in the plots. The minimum inter-plot distance in the sampling areas was 150 m. Plant species were identified by a plant taxonomist, and through the use of herbarium specimens and identification guides (Hawthorne & Jongkind, 2006; Hawthorne, 1990).

Data analysis

Community structure

We calculated species richness and Shannon diversity index in the forest sites. A rarefaction-extrapolation technique was used to standardise species richness based on a constant number of individuals using iNEXT package in R. We tested the significance of the differences in Shannon diversity index among the forest sites using permutation tests in PAST statistical package version 2.17c (Hammer et al., 2001).

Community abundance of lianas was compared among the forest sites by running nested ANOVA, where sampling area was nested within forest site. We employed aov function in the stats package in R to perform the nested ANOVA. Using the equation of Harper et al. (2005, 2015), we calculated magnitude of edge influence (MEI) on abundance for individual liana species with abundance [?] 10 stems. The equation is given as:$MEI = \frac{e-i}{e+i}$, where e = species abundance in edge site, and i = species abundance in non-edge site, which was obtained by finding the average of the values of interior and deep-interior sites. The values of MEI ranges from -1 (negative edge influence) to +1 (positive edge influence). MEI value of zero indicates no edge influence. The strength of MEI was determined as follows (Ofosu-Bamfo et al., 2019): 0 (no edge influence), [?]0.19 (very weak), 0.20–0.39 (weak), 0.40–0.59 (moderate), 0.60–0.79 (strong), 0.80–1.0 (very strong).

Network structure of liana-tree interactions

Liana-tree network structure was quantified using the following network metrics: nestedness, modularity, degree of specialization (H2', d'), connectance, module connectivity and interactions (c and z values), species co-occurrence. We used quantitative liana-tree species matrices except in the species co-occurrence test where binary matrices were employed. Each of matrices was made up of liana species assigned to rows and tree species assigned to columns. We also represented the various networks in graphs using plotweb function in the bipartite package in R.

Nestedness

Nestedness occurs when the more specialist species interact only with subsets of the species interacting with the more generalist species (Bascompte et al., 2003; Ponisio et al., 2019). This means that generalists interact with one another, and specialists tend to interact with generalists, but specialist-specialist interactions are often absent (Bascompte et al., 2003). We calculated weighted nestedness metric, WNODF with the networklevel function in bipartite package in R (Dormann et al., 2020), in accordance with the nestedness equation of Almeida-Neto and Ulrich (2010). The WNODF metric ranges from 0 (fully non-nested) to 100 (fully nested). There are two forms of non-nested pattern described in literature: (1) when nestedness value is consistent with the null model expectation, and (2) when nestedness value is significantly less than that of the null model. The aforementioned patterns of nestedness refer to two different community assembly (random and non-random assembly, respectively) and therefore must be distinguished. We therefore used anti-nestedness to refer to the situation where observed nestedness values were significantly lower than those expected by chance, while we referred to networks that presented observed nestedness values which were consistent with null model expectation as not nested.

Degree of specialisation

The degree of specialisation was determined for the various networks and the individual species in the networks as follows:

Using the H2' index, we quantified network specialisation of the various forest sites. The index measures the extent to which observed interactions deviate from the interactions that would be expected given the marginal totals of the interactions per species (Bluthgen et al., 2006). Generally, higher values of the H2' index indicate that the species in the network are more selective, resulting in higher specialisation of the network. The index ranges from 0 (no specialisation) to 1 (complete specialisation). The H2' index was run with H2fun function in the bipartite package.

The degree of species specialisation was determined by calculating d' index, using dfun function in the bipartite package. This index is defined as the deviation from a conformity expected by the overall utilisation of potential partners (Bluthgen et al., 2007).

Network connectance

Weighted connectance was calculated to express network connnectance in the study. It is defined as the linkage density divided by number of species in the network (Dormann et al., 2020; van Altena et al., 2016).

The values of weighted connectance range from 0 (no interaction) to 1 (perfectly connected). Weighted connectance was run with the networklevel function in the bipartite package.

Modularity

We measured modularity index (Q) with the DIRTLPAwb+ algorithm using computeModules function within the bipartite package (Beckett, 2016). Modularity measures the tendency of a network to form modules of interacting species, which interact more with one another than with species of other modules (Carstensen et al., 2016; Dormann et al., 2020). The Q index ranges from 0 for networks with clustering not different from random to 1 for networks with perfect modules. The Q index calculation followed the equations in Newman (2006).

Test of statistical significance of the metrics

The above mentioned network metrics were tested for their statistical significance by generating 1,000 null models and comparing them with the observed metric values using the Patefield algorithm (Patefield, 1981) in the bipartite package.

Module connectivity and interactions

The topological roles of liana and tree species with respect to network modularity was assessed based on the number of links of the species. We achieved this by calculating the weighted standardised among-module connectivity (c) and within-module interactions (z), using species strength of interaction (Watts et al. 2016). To obtain the corresponding appropriate c and z thresholds for the species, we generated 100 null models of the original networks using DIRTLPAwb+ algorithm, and 95 % quantiles as threshold c- and z-values. Based on the c and z values generated, the species were grouped into four categories of topological roles (Olesen et al., 2007) indicated below:

1. Peripherals: species with lower c- and z-values compared to the threshold values.
2. Network hubs: species with higher c- and z-values compared to the threshold values.
3. Connectors: made up of species with higher c-values and lower z-values compared to the threshold values.
4. Module hubs: made up of species with higher z-values and lower c-values compared to the threshold values.

Species co-occurrence

Liana species co-occurrence patterns were determined with the cooc_null_model function from EcoSimR package (Gotelli et al., 2015). We used the C-score metric, which is the average number of checkerboards for two species (Stone & Roberts, 1990), to measure species co-occurrence. The metric was calculated according to the equation described by Almeida-Neto & Ulrich (2011). To assess the patterns of co-occurrence, 10,000 null models were generated by the quasiswap algorithm and compared with the observed c-score values. The c-score measures the tendency of species to not co-occur (Stone & Roberts, 1990). Thus, the greater the c-score in relation to the null model, the greater the tendency of the species to not co-occur (i.e., segregation), and the smaller the c-score value in relation to the null model, the higher the tendency of species to co-occur (i.e., aggregation).

RESULTS

Liana community structure

There were more liana species in edge habitat than interior habitat, which in turn had more species than deep-interior site in the Asenanyo Forest Reserve (Table 1). Both the rarefaction and extrapolation curves attested to this observation (Figure 1a). The rarefaction curves did not reach asymptote, showing there could be more undetected species in the forest sites. The species in edge, interior and deep-interior sites belonged to 28 genera and 15 families, 26 genera and 16 families, and 24 genera and 12 families, respectively. Edge and interior sites had similar Shannon diversity index ($P = 0.691$; H' = 2.93 and 2.91, respectively), while each of them supported significantly higher Shannon diversity index than deep-interior site (H' = 2.74) (P = 0.004 and 0.010, respectively). Species evenness (E) was similar among all the forest sites in the Asenanyo Forest Reserve ($P > 0.05$; edge: E = 0.48, interior: E = 0.51, deep-interior: E = 0.53).

Within the Suhuma Forest Reserve, liana species richness was comparable among the three forest sites (Table 1). The identified liana species belonged to 29 genera and 15 families in edge site, 27 genera and 13 families in interior site, and 27 genera and 16 family in deep-interior site. The rarefaction and extrapolation curves of the forest sites depicted a similar trend, with the curves showing that there could be more undetected species in the forest sites (Figure 1b). Shannon diversity index in edge site (H'= 2.99) did not vary from that in interior site (H' = 3.01) (P = 0.723). However, due to significantly higher species evenness in deep-interior site ($P < 0.05$; deep-interior: E = 0.59, edge: E = 0.45, interior: E = 0.50), it supported significantly higher Shannon diversity index (H' = 3.20) than edge (P = 0.004) and interior (P = 0.027) sites.

The five most abundant liana species in edge and interior sites of the Asenanyo Forest Reserve were *Millettia chrysophylla* ,*Salacia elegans* , *Griffonia simplicifolia* , *Alafia barteri* and *Motandra guineensis* (Table 1). They contributed 54.5 and 54.3 % of total liana abundance in edge and interior sites, respectively. The 10 most abundant species in these sites contributed 74.9 and 74.8 % of the liana stems in edge and interior sites, respectively. All the above mentioned species also constituted the five most abundant species in interior site. Four of the above mentioned species namely, *M . chrysophylla* , *G .simplicifolia* , *A . barteri* , and *S .elegans* , together with *Strophanthus preussii* were the five most abundant species in deep-interior site, forming 58.3 % of the stems in this site. The 10 most abundant species in deep-interior site constituted 80.6 % of the total stems in the site.

In the Suhuma Forest Reserve, *M . chrysophylla* , *G .simplicifolia* , *M . guineensis* , *Calycobolusafricanus* and *A . barteri* were the five most abundant species in edge site, constituting 54.8 % of liana stems in the site (Table 1). The stems of the 10 most abundant species were 72.9 % of the liana abundance in edge site. In interior site, the five most abundant species included four of the above mentioned species in edge site (i.e., *M . chrysophylla* , *G .simplicifolia* , *C . africanus* , *M .guineensis*) and *Acacia pentagona* . The abundance of these five species was 52.3 % of the total abundance in interior site. With regard to the 10 most abundant species, they contributed 75.3 % of the liana abundance in the site. *M . chrysophylla* , *A .pentagona* , *G . simplicifolia* , *C .africanus* , and *A . barteri* formed the five most abundant species in deep-interior site, by contributing 41.3 % of the liana stems in deep-interior site. In the same forest site, the 10 most abundant species contributed 65.8 % of the total liana stems in the site.

Liana abundance differed significantly between edge and deep-interior sites of the Asenanyo (F = 3.84; P = 0.041) and Suhuma (F = 6.05; P = 0.010) Forest Reserves (Table 1). Nonetheless, there were no significant differences in liana abundance among the other forest sites. In both forest reserves, there was no significant effect of sampling site on liana abundance (Asenanyo: F = 0.091, P = 0.964; Suhuma: F = 2.16, 0.128). MEI in the Asenanyo Forest Reserve ranged from -1 to 0.92 (Table 1). More species experienced positive MEI on their abundance than those that had negative MEI on their abundance. *Caesalpinia cucullata*and *Combretum acutum* were the only species that experienced very strong MEI in the Asenanyo Forest Reserve. *Paullinia pinnata* was the only species with strong MEI on its abundance. The rest of the species recorded moderate, weak, and very weak MEI on their abundance. On the contrary, *A . pentagona* had no MEI on its abundance. In Suhuma Forest Reserve the MEI on liana species abundance ranged from -0.43 to 0.45 (Table 1). Liana species abundance experienced both positive and negative MEI, with the majority of the species experiencing positive MEI. Nevertheless, there was no MEI on the abundance of*Strophanthus sarmentosus* in the Suhuma Forest Reserve. There was moderate MEI on the abundance of *Manniophyton fulvum* and*Neuropeltis prevosteoides* , while the MEI on the abundance of the remaining species was either weak or very weak.

Network metrics

We observed 179 interactions between 40 liana species and 38 tree species in edge site of Asenanyo Forest Reserve (Appendix 1a). A total of 123 and 119 interactions were recorded in interior (involving 34 liana species and 28 tree species; Appendix 1b) and deep-interior (between 31 liana species and 35 tree species; Appendix 1c), respectively. On the part of Suhuma Forest Reserve, 44 liana species interacted with 63 tree species in edge site and produced a total of 202 interactions (Appendix 1d). In interior site, 44 liana species interacted with 46 tree species, resulting in 173 interactions (Appendix 1e). We recorded an interaction involving 42 liana species and 46 tree species in deep-interior site, giving rise to 175 interactions (Appendix 1f).

In the Asenanyo Forest Reserve, the observed nestedness metric was significantly lower than the means of the null model in the three forest sites (Table 2). Likewise, the liana-tree networks were less connected than the null models of the three networks. However, the three networks were more modular and specialised compared to the null networks. The significant modularity of the networks resulted in the formation of a number of modules in edge site (14 modules), which was more than the number of modules in deep-interior (11 modules), which in turn, was more than that in interior site (7 modules) (Figure 2a-c; Appendix 2). The size of the modules varied greatly in the networks, ranging from 2-13 species in edge site, 5-13 species in interior site, and 2-12 species in deep-interior site.

We did not observe significant differences in nestedness between the observed and null models in the three forest sites in the Suhuma Forest Reserve. Nevertheless, the three liana-tree networks in the forest recorded significantly higher modularity and specialisation than expected by chance. The networks in deep-interior forest site (deep-interior: 14 modules) exhibited higher number of modules than the other sites (edge site: 9 modules, interior site: 9 modules) (Figure 3a-c; Appendix 2). Furthermore, the networks showed much variation in the size of the modules (edge: 5-19 species, interior: 6-15 species, deep-interior: 3-11 species). Connectance of the three networks was significantly lower than that of the null models. The specialisation asymmetric values of the networks in the Asenanyo Forest Reserve were close to zero, indicating weak asymmetry. The specialisation asymmetry value of interior site network was consistent with that of the null model; those of the other networks were significantly higher than randomised expectations. The networks in the Suhuma Forest Reserve did not only show weak asymmetry, but they also did not differ significantly from that expected by chance.

Species specialisation metric

The degree of specialisation differed considerably among the species in the three forest sites within the Asenanyo Forest Reserve. The majority of the liana species (edge: 61.5 %, interior: 55.9 %, deep-interior: 63.3 %) had significantly higher degree of specialisation than that of the respective null models (Appendix 3). Correspondingly, the degree of specialisation varied widely among the species in the forest sites of the Suhuma Forest Reserve. Most of the species in edge (58.1 %) and deep-interior (65.0 %) sites were significantly more specialised than expected by chance. The minority of the tree species in the three sites of Asenanyo and Suhuma Forest Reserve were more specialised than expected by chance (Appendix 4). About 43 % of liana species in interior site had significantly higher degree of specialisation than the null model. In the Asenanyo Forest Reserve, the proportion of tree species with higher specialisation than their null models (edge: 42.1 %, interior: 42.9 %, deep-interior: 37.1 %) was lower than the proportion of tree species that did not show higher specialisation than expected by chance. A similar trend was recorded in the Suhuma Forest Reserve (edge: 36.5 %, interior: 39.1 %, deep-interior: 45.7 %). Generally, higher proportions of lianas than tree species showed higher specialisation than the null models.

Species topological roles in the networks

In the Asenanyo Forest Reserve, liana species in edge site were mainly peripherals, with the exception of four species (*C .cucullata* , *M . chrhysophylla* , *M .guineensis* , *Morinda morindoides*) which acted as connectors (Figure 4a). *Millettia lutens* and *Tiliacora dielsiana* were the only module hub species of lianas in edge site. Network hubs did not occur among lianas in edge site. The connector and module hub species constituted 15.4 % of liana species in this site. The majority of the tree species also performed specialist role in edge site, but seven of the species (*C . mildbraedii* ,*Hymenostegia afzelii* , *Trilepisium* sp., *Baphia nitida* , *Entandrophragma utile* , *Triplochiton scleroxylon* ,*N . papaverifera*) were connectors (Figure 5a).

These generalist species formed 25 % of the tree species. In interior site, we had no liana connectors and network hubs, but two module hubs existed in this site (*M . guineensis* , *S . elegans*), making up 5.6 % of liana species in interior site (Figure 4b). The rest of the liana species served as peripherals in interior site. Trees in interior site were mostly peripherals, with only one connector (*Albizia zygia*) and one module hub (Bec) species (Figure 5b), but no network hub trees. These generalists were 5.7 % of the total tree species in this site. Within deep-interior site, we recorded two liana connectors *(G . simplicifolia* and *S .preussii)* and one liana module hub (*S . elegans*) (Figure 4c), which together made up 10.3 % of the liana species in the site. The rest of the liana species in deep-interior site were peripherals. There were three connectors (*C . mildbraedii* ,*Amphimas pterocarpoides* , *Turraeanthus africanus*) and one module hub of tree species (*Homalium dewevrei*) in deep-interior site, but there was no network hub species (Figure 5c). These tree species composed of 8.6 % of the total number of species in deep-interior site.

We recorded *G . simplicifolia* , *C . tarquense* ,*A . kamerunensis* and *Combretum paniculatum* as connector liana species within edge site of the Suhuma Forest Reserve, while the majority of the liana species were peripherals (Figure 6a).*C . africanus* was a network hub in the edge site. The above mentioned generalists constituted 11.4 % of the total liana species. Five tree species acted as connectors in edge site (*C .mildbraedii* , *Celtis philippensis* , *Entandrophragma angolense* , *N . papaverifera* , *Trichilia prieuriana*), while one tree species was identified as a module hub (*Calpocalyxbrevibracteatus*) (Figure 7a). Network hubs of tree species were not recorded in edge site. Together, the connector and module hub species formed 9.5 % of the total number of tree species in edge site. In interior site of Suhuma Forest Reserve, most of the liana species were peripherals. Generalist liana species were module hubs (*A .pentagona* , *C . africanus* , *N .acuminata* , *M . fulvum*) and network hub (*M .chrysophylla*), but with no connector species (Figure 6b). The above mentioned generalist species formed 12.2 % of liana species in interior site. The majority of the tree species in interior site of Suhuma Forest Reserve acted as peripherals. We did not identify connector tree species in this site, but a few module hub species occurred there (*Albizia adianthifolia* , *C .mildbraedii* , *Sterculia oblonga*) (Figure 7b). These generalist species formed 6.5 % % of the tree species. In deep-interior site, lianas were mainly peripherals, except for *G .simplicifolia* , *C . africanus* , *Neuropeltis prevosteoides* and *Alafia* sp., that acted as connectors (Figure 6c). The above-mentioned generalists formed about 9.8 % of the total liana species. Tree species in deep-interior site were generally peripherals, except *C . mildbraedii* and *Ricinodendron heudelotii* (connectors), and Amp and Gut (module hubs) which formed 8.7 % of the tree species (Figure 7c).

Species co-occurrence of lianas

In the Asenanyo Forest Reserve, the observed c-score of the matrix in edge site was significantly lower than the mean of the null model (Table 2). Nevertheless, the c-scores of the observed matrices in interior and deep-interior sites was consistent with the simulated mean c-scores. In all the three sites in the Suhuma Forest Reserve, the observed c-score values were not significantly different from those expected by chance.

DISCUSSION

Liana community structure

Our study showed contrasting edge effects on species diversity in the two moist semi-deciduous forests. In the Asenanyo Forest Reserve, edge appeared to have enhanced diversity, while an opposite trend occurred in the Suhuma Forest Reserve. The trend in the Asenanyo Forest Reserves is consistent with previous studies that also recorded higher liana diversity at forest edges in relation to forest interiors (Addo-Fordjour & Owusu-Baodi 2016; Laurance et al., 2001). It is important to note that edge effect in our study was observed in edge site in relation to only deep-interior site. Therefore, we did not observe variation in species diversity between edge and interior sites. This trend is an indication that edge effects on liana species diversity penetrated 200 m into the interior of the forest. The findings of the present study also indicated that species evenness was poorer in edge site of the Suhuma Forest Reserve, resulting in a lower species diversity, irrespective of its higher species richness. The forest edge appears to have influenced species evenness by exerting differential effects on the abundance of different species in edge site. Thus, in edge site of Suhuma Forest Reserve, changes in species abundance mediated edge effects on liana species diversity. The observed species diversity variation may possibly relate with edge-related changes in variables such as microclimate, and tree density and mortality that often characterise forest edges (Ofosu-Bamfo et al., 2019; Wekesa et al., 2019).

Our study revealed pronounced edge effect on liana abundance at the community level in the two forest reserves. This pattern is supported by previous studies which showed that edge effect enhanced liana abundance in their respective forests (Addo-Fordjour & Owusu-Boadi, 2016; Campbell et al., 2018; Laurance et al., 2001). Our results showed that in both forest reserves, edge effects penetrated 200 m from the edge, and this is in keeping with Laurance et al. (1991) who reported that edge effects on the abundance of disturbance-adapted plants such as lianas can penetrate 200 m into forest interior. Forest edges are often characterised by increased levels of light and desiccation or dryness, which can promote liana increase (Campbell et al., 2018). Given that there was a sharp contrast between our forest edges and the surrounding matrix, we expected the above mentioned conditions to be more pervasive in edge site. Thus, increased levels of light and dryness at the forest edge may be associated with the positive response of liana abundance to edge disturbance in the two forests. At the species level, many liana species showed diverse responses to edge disturbance in the two forests. The values of MEI with respect to species abundance varied widely among the liana species. A similar finding was reported in two rainforests in Ghana (Ofosu-Bamfo et al., 2019). Our finding implies that although optimal light and dry conditions may characterise forest edge sites, they may not enhance the proliferation of some liana species. This may occur when there is excessive soil desiccation causing liana mortality (Nepstad et al., 2007). Nevertheless, some of the liana species showed high positive MEI, indicating that they tended to prefer edge sites.

Liana-tree network structure

We found anti-nested and modular structure in the three liana-tree interaction networks in Asenanyo Forest Reserve. This trend has also been reported by Addo-Fordjour et al. (2021, 2016), and to some extent by Magrach et al. (2016) whose liana-tree networks showed anti-nested structure (see supplementary data). Nevertheless, our study is at variance with that of Sfair et al. (2010) which recorded nested structure in three distinct vegetation formations in Brazil, and also differs from the networks of Sfair et al. (2015) which did not show modularity. In the suhuma Forest Reserve, all the three networks were not nested but modular. Though the two nestedness patterns shown by the networks in the Asenanyo and Suhuma Forest Reserves refer to non-nested structure, that of the former depicts non-random assembly of species whereas the latter indicates random assembly of species. We argue that a clear distinction should be made between the two types of non-nestedness in network studies so that the distribution pattern of each of them would be fully understood. The presence of non-significant nestedness in the Suhuma Forest Reserve may be due to differences in liana species ability to colonise host trees and/or the use of defense strategies of hosts to avoid lianas (Addo-Fordjour et al., 2016; Genini et al., 2012). As a recap, a nested structure is formed when there are interactions involving generalists and generalists, and specialists and generalists, but no interaction of specialists and specialists (Landi et al., 2018). Staniczenko et al. (2013) showed that for a nested quantitative network, interactions of generalist-generalist species are strongest, followed by those of generalist-specialist species, with no specialist-specialist interactions (or when present with much weaker interactions). Thus, for a nested structure to occur in a quantitative network like ours, there should be a good number of specialist and generalist species undergoing interactions. However, in our networks, we observed only a few generalists of lianas and trees that interacted, but with many specialist species interacting among themselves. This situation increased the likelihood of specialist-specialist interactions at the expense of generalist-generalist and generalist-specialist interactions, resulting in absence of nested structure in the various networks. A similar trend was observed in mycorrhizal networks (Jacquemyn et al., 2015). The specialist-specialist interactions in our networks may account for the non-asymmetry and weak asymmetry exhibited by the networks. This finding shows that our networks tended to be more symmetric in their interactions, a trend which causes non-significant nestedness and significant modularity in ecological networks (Guimaraes et al., 2007). Overall, the findings on liana-tree network structure reported in the current and previous studies show that there is no universal pattern in the structure of liana-tree interactions. The patterns obtained may be dependent on the network complexity, and species traits and abundance, which are known to influence the organisation of liana-tree interactions (Sfair et al. 2018, 2010). The existence of high modular structure in the various networks may increase their stability and robustness by limiting diffusion of perturbations through network (Thebault & Fontaine, 2010). This may explain why the patterns of network structure in edge site was consistent with those in interior and deep-interior sites, irrespective of disturbance at edge site. The modular structure of our networks may help conserve the networks of species interaction, which in turn, may lead to the conservation and maintenance of ecosystem functioning.

Though the nature of liana-tree interaction is still a subject of debate, it tends to be antagonistic, in view of the fact that lianas are not only structural parasites of trees (Tang et al., 2012), but also compete intensely with trees for resources (Sfair et al., 2018). Species of antagonistic networks often evolve high specialisation in order to survive the antagonism of the interactions (Maliet et al., 2020). Our results revealed strong species and network specialisation in the forest sites, which demonstrates the existence of strong liana-host specificity across the various networks in the two forest. Host specificity and network specialisation have been reported to cause non-nestedness and modularity in networks (Cordeiro et al., 2020; Dallas & Cornelius, 2015; Wardhaugh et al., 2015; Maliet et al., 2020). Given this information, the non-nested and modular structure observed in our networks may be driven by the specialisation of the networks and host specificity of the liana species. The specialisation in the liana-tree networks may be related to co-evolution in lineages of lianas and trees in the networks (Sfair et al., 2015). The possibility of co-evolution of lianas and trees in our networks is supported by Ponisio et al. (2019, 2017) who showed that ecological communities that co-evolve become more anti-nested and modular over time. Montoya et al. (2015) found out that functional group diversity increases with modularity in complex networks, and that functional groups form modules in communities. In this regard, the presence of high number of modules per network in the forest sites may reflect the existence of different liana functional groups that interact with tree communities in the forests. Such networks with high level of modularity may possess increased resistance to disturbance (Olesen et al., 2007; Saunders & Rader, 2019). Differences in colonisation rates in fish parasites were found as a cause of anti-nested structure in such networks (Poulin & Guegan, 2000). In each of the networks, different liana species showed varying degree of specialisation, while others exhibited generalisation. This phenomenon suggests that the rate of colonisation would differ markedly among the species, with highly specialised species having lower rate of colonisation, while species with low specialisation, or generalisation exhibit higher colonisation rate. In this regard, like the parasite-fish network (Poulin & Guegan, 2000), the anti-nested structure in our networks could have partly been occasioned by variation in colonisation rates of the liana species. Generally, our study adds to the number of studies that have demonstrated the existence of non-nestedness and modularity in liana-tree networks (e.g., Addo-Fordjour et al., 2021; Magrach et al., 2016).

Species role in the networks

The finding of the current study showed that lianas and trees were predominantly specialists (i.e., peripherals), irrespective of edge disturbance or edge effects, indicating possible robustness of species roles to disturbance. A similar pattern was recorded in a moist semi-deciduous forest in Ghana (Addo-Fordjour et al., 2021). The high specialisation of the species in the networks shows that antagonism in the networks might have resulted in the evolution of specialisation in both liana and tree species (Maliet et al., 2020). The role of some of the liana and tree species was consistent in the forest sites, whiles other species roles changed from one site to another. This phenomenon indicates that edge effects probably caused a switch in the role of some of the species among the forest sites, while the role of other species remained unchanged. The change from specialist to generalist and vice versa, and from one form of generalist to another may be related to changes in species abundance and distribution following edge disturbance (Addo-Fordjour et al., 2021). Some of the species identified as structural important species (i.e., connectors, module hubs, network hubs) in our study were also reported as species that possessed structural importance in a moist semi-deciduous forest in Ghana (Addo-Fordjour & Afram, 2021). These plants which include two liana species (*G . simplicifolia* , *C . africanus*) and three tree species (*T . scleroxylon* , *N .papaverifera* , *C . mildbraedii*) may have unique functional roles that support the functioning of the forests.

Species co-occurrence of lianas

Generally, lianas were assembled randomly on their hosts in most of the forest sites, suggesting that chance events rather than edge disturbance, determined liana distribution on trees. Thus, we argue that the liana communities might have been assembled on trees by stochastic processes including host characteristics. Our finding is consistent with that reported in a semi-deciduous forest in Brazil (Zulqarnain et al., 2016). Contrary to the above, liana species in edge site of Asenanyo Forest Reserve showed positive species co-occurrence on their hosts. Since this network was organised into modules, the positive co-occurrence trend could have existed within the modules. Thus, in the modules, liana species resorted to positive or facilitative interactions (McGarvey & Veech, 2018), that might have arisen deterministically. At forest edges, there is usually an elevated level of light coupled with dry conditions, and trellis availability, all of which can work together to enhance liana proliferation (Campbell et al., 2018). It appears that as these resources are increased at edge, lianas tend to share rather than compete for them, resulting in their positive co-occurrence on the host trees. The liana species aggregation on trees could have also arisen by facilitation, where increasing liana abundance at edge site would cause new liana individuals to use already established stems to climb trees (Perez-Salicrup & Sork, 2001).

CONCLUSION

The findings of the study revealed considerable edge effects on liana diversity and abundance in the two moist semi-deciduous forests. Despite the enhanced diversity and abundance in edge site of each forest, the patterns of liana-tree network structure of edge site were similar to those in interior and deep-interior sites. All the networks in the two forests were less connected and non-nested, but modular and specialised. Lianas were mostly randomly distributed on host trees in all the forest sites except edge site in the Suhuma Forest Reserve. Topologically, the majority of liana and tree species were peripherals (i.e., specialist), but a few species tended to be generalists, acting as connectors, module hubs and network hubs. The role of most of the species did not change from one site to another, even though the topological role of a few species changed from one site to another. Overall, our study shows that liana community structure was more susceptible to forest edge than liana-tree network structure. The findings of our study corroborate previous studies, and also present unique findings related to liana-tree network structure. Our findings which enhance our understanding of liana-tree interactions, have conservation implications relating to stability and robustness of the networks. Finally, the findings of the present study can potentially contribute to a robust edge theory development.

AKNOWLEDGEMENTS

The authors are grateful to the Forestry Commission of Ghana for providing access to the forest reserves.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Bismark Ofosu-Bamfo: Methodology (supporting); Investigation (lead); Formal analysis (supporting); writing – original draft (equal); writing – review and editing (supporting). **Patrick Addo-Fordjour:** Conceptualisation (lead); Methodology (lead); Supervision (equal); Formal analysis (lead); writing – original draft (equal); writing – review and editing (lead). **Ebenezer J.D. Belford:** Conceptualisation (supporting); Methodology (supporting); Supervision (equal); writing – review and editing (supporting).

DATA AVAILABILITY STATEMENT

Data associated with the manuscript will be available on Dryad.

REFERENCES

Addo-Fordjour, P. and Owusu-Boadi, K., 2016. Linear edge effects on liana and tree communities in two tropical forest ecosystems in Ghana. *Ecological research* , *31* (5), 709-718.

Addo-Fordjour, P., Agyei, L.A., Ofosu-Bamfo, B., Issifu, I.N., Osei, G.O., Appiah-Kubi, R., Bremang, E.K. and Kroduah, P.O., 2021. Temporal dynamics of liana communities in moist semi-deciduous forest stands with different management histories in Ghana. *Forest Ecology and Management* , *489* , 119042.

Addo-Fordjour, P., Rahmad, Z.B. and Shahrul, A.M.S., 2016. Liana species composition, dominance and host interactions in primary and secondary forests in Malaysia. *Tropical Ecology* , *57* (3).

Addo-Fordjour, P. and Afram, I.S., 2021. Clearcutting and selective logging have inconsistent effects on liana diversity and abundance but not on liana–tree interaction networks. *Biotropica* , 53, 442-452.

Almeida-Neto, M. and Ulrich, W., 2010. A straightforward computational approach for quantifying nestedness using abundance data. *Environmental Modelling & Software* , *26* (2), 173-178.

Aragon, G., Abuja, L., Belinchon, R., Martinez, R. 2015. Edge type determines the intensity of forest edge effect on epiphytic communities. *European Journal of Forest Research,* 134, 443–451

Bascompte, J., Jordano, P., Melian, C.J. and Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences* , *100* (16), 9383-9387.

Beckett, S.J., 2016. Improved community detection in weighted bipartite networks. *Royal Society open science* , *3* (1), 140536.

Blick, R. and Burns, K.C., 2009. Network properties of arboreal plants: are epiphytes, mistletoes and lianas structured similarly? *Perspectives in Plant Ecology, Evolution and Systematics* , *11* (1), 41-52.

Blick, R.A.J. and Burns, K.C., 2011. Liana co-occurrence patterns in a temperate rainforest. *Journal of Vegetation Science* , *22* (5), 868-877.

Bluthgen, N., Menzel, F. and Bluthgen, N., 2006. Measuring specialization in species interaction networks. *BMC ecology* , *6* (1), 1-12.

Bluthgen, N., Menzel, F., Hovestadt, T., Fiala, B. and Bluthgen, N., 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Current biology* , *17* (4), 341-346.

Campbell, M.J., Edwards, W., Magrach, A., Alamgir, M., Porolak, G., Mohandass, D. and Laurance, W.F., 2018. Edge disturbance drives liana abundance increase and alteration of liana–host tree interactions in tropical forest fragments. *Ecology and Evolution* , *8* (8), 4237-4251.

Carstensen, D.W., Sabatino, M. and Morellato, L.P.C., 2016. Modularity, pollination systems, and interaction turnover in plant-pollinator networks across space. *Ecology* , *97* (5), 1298-1306.

Castledine, M., Sierocinski, P., Padfield, D. and Buckling, A., 2020. Community coalescence: an eco-evolutionary perspective. *Philosophical Transactions of the Royal Society B* , *375* (1798), 20190252.

Cordeiro, J., de Oliveira, J.H., Schmitz, H.J. and Vizentin-Bugoni, J., 2020. High niche partitioning promotes highly specialized, modular and non-nested florivore–plant networks across spatial scales and reveals drivers of specialization. *Oikos* , *129* (5), 619-629.

Dallas, T. and Cornelius, E., 2015. Co-extinction in a host-parasite network: identifying key hosts for network stability. *Scientific reports* , *5* (1), 1-10.

Dormann, C.F., 2020. Using bipartite to describe and plot two-mode networks in R. *R package* .

Dovčiak, M. and Brown, J., 2014. Secondary edge effects in regenerating forest landscapes: vegetation and microclimate patterns and their implications for management and conservation. *New forests* , *45* (5), 733-744.

Fagan, W.F., Cantrell, R.S. and Cosner, C., 1999. How habitat edges change species interactions. *The American Naturalist* , *153* (2), 165-182.

FAO and UNEP. 2020. *The State of the World's Forests 2020. Forests, biodiversity and people* . Rome.

Genini, J., Côrtes, M.C., Guimarães Jr, P.R. and Galetti, M., 2012. Mistletoes play different roles in a modular host–parasite network. *Biotropica* , *44* (2), 171-178.

Gotelli, N., Hart, E., Ellison, A. and Hart, M.E., 2015. Package "EcoSimR"—null model analysis for ecological data. *R Package.*

Guimarães Jr, P.R., Sazima, C., Reis, S.F.D. and Sazima, I., 2007. The nested structure of marine cleaning symbiosis: is it like flowers and bees?. *Biology Letters* , *3* (1), 51-54.

Hammer, Ø., Harper, D.A. and Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica* , *4* (1), 9.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D.A.R., Jaiteh, M.S. and Esseen, P.A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation biology* , *19* (3), 768-782.

Harper, K.A., Macdonald, S.E., Mayerhofer, M.S., Biswas, S.R., Esseen, P.A., Hylander, K., Stewart, K.J., Mallik, A.U., Drapeau, P., Jonsson, B.G. and Lesieur, D., 2015. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in C anada and F ennoscandia. *Journal of Ecology* , *103* (3), 550-562.

Hawthorne, W., 1990. *Field guide to the forest trees of Ghana* . Overseas Development Administration.

Hawthorne, W.D. and Jongkind, C.C., 2006. *Woody plants of Western African forests, A guide to the forest trees, shrubs and lianes from Senegal to Ghana* . Royal Botanic Gardens, Kew.

Hawthorne, W.D., Abu-Juan M., 1995. Forest protection in Ghana. IUCN Gland, Switzerland and Cambridge, UK.

Hawthorne, W.D., 1996. Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences* , *104* , 75-176.

Jacquemyn, H., Brys, R., Waud, M., Busschaert, P. and Lievens, B., 2015. Mycorrhizal networks and coexistence in species-rich orchid communities. *New Phytologist* , *206* (3), 1127-1134.

Landi, P., Minoarivelo, H.O., Brannstrom, A., Hui, C. and Dieckmann, U., 2018. Complexity and stability of adaptive ecological networks: a survey of the theory in community ecology. *Systems analysis approach for complex global challenges* , 209-248.

Laurance, W.F., 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biological conservation* , *57* (2), 205-219.

Laurance, W.F., Nascimento, H.E., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E. and Capretz, R.L., 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* , *87* (2), 469-482.

Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. and Lovejoy, T.E., 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* , *82* (1), 105-116.

Magrach, A., Senior, R.A., Rogers, A., Nurdin, D., Benedick, S., Laurance, W.F., Santamaria, L. and Edwards, D.P., 2016. Selective logging in tropical forests decreases the robustness of liana–tree interaction networks to the loss of host tree species. *Proceedings of the Royal Society B: Biological Sciences* , *283* (1826), 20153008.

Maliet, O., Loeuille, N. and Morlon, H., 2020. An individual-based model for the eco-evolutionary emergence of bipartite interaction networks. *Ecology Letters* , *23* (11), 1623-1634.

Martino, R.M., 2015. Matrix and Edge Effects on the Maintenance of Ecological Function in an Afromontane Protected Area.

Massol, F., Dubart, M., Calcagno, V., Cazelles, K., Jacquet, C., Kefi, S. and Gravel, D., 2017. Island biogeography of food webs. *Advances in ecological research* , *56* , 183-262.

McGarvey, D.J. and Veech, J.A., 2018. Modular structure in fish co-occurrence networks: A comparison across spatial scales and grouping methodologies. *Plos one* , *13* (12), p.e0208720.

Medoc, V., Firmat, C., Sheath, D.J., Pegg, J., Andreou, D. and Britton, J.R., 2017. Parasites and biological invasions: predicting ecological alterations at levels from individual hosts to whole networks. *Advances in Ecological Research* , *57* , 1-54.

Mohandass, D., Hughes, A.C., Campbell, M. and Davidar, P., 2014. Effects of patch size on liana diversity and distributions in the tropical montane evergreen forests of the Nilgiri Mountains, southern India. *Journal of Tropical Ecology* , 579-590.

Montoya, D., Yallop, M.L. and Memmott, J., 2015. Functional group diversity increases with modularity in complex food webs. *Nature communications* , *6* (1), 1-9.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in ecology & evolution* , *10* (2), 58-62.

Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P. and Cardinot, G., 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* , *88* (9), 2259-2269.

Newman, M.E., 2006. Modularity and community structure in networks. *Proceedings of the national academy of sciences* , *103* (23), 8577-8582.

Ofosu-Bamfo, B., Addo-Fordjour, P. and Belford, E.J., 2019. Does road-edge affect liana community structure and liana-host interactions in evergreen rainforests in Ghana?. *Acta Oecologica* , *101* , 103476.

Olesen, J.M., Bascompte, J., Dupont, Y.L. and Jordano, P., 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences* , *104* (50), 19891-19896.

Patefield, W. M. (1981). Algorithm AS 159: An efficient method of generating r x c tables with given row and column totals. *Journal of Applied Statistics* , *30* , 91–97.

Pedro, M.S., Rammer, W. and Seidl, R., 2015. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia* , *177* (3) 619-630.

Perez-Salicrup, D.R., Sork, V.L. and Putz, F.E., 2001. Lianas and Trees in a Liana Forest of Amazonian Bolivia 1. *Biotropica* , *33* (1), 34-47.

Ponisio, L.C. and M'Gonigle, L.K., 2017. Coevolution leaves a weak signal on ecological networks. *Ecosphere* , *8* (4), e01798.

Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimaraes Jr, P.R., Hembry, D.H., Morrison, B. and Gillespie, R., 2019. A network perspective for community assembly. *Frontiers in Ecology and Evolution* , *7* , 103.

Porensky, L.M., 2011. When edges meet: interacting edge effects in an African savanna. *Journal of Ecology* , *99* (4), 923-934.

Poulin, R. and Guegan, J.F., 2000. Nestedness, anti-nestedness, and the relationship between prevalence and intensity in ectoparasite assemblages of marine fish: a spatial model of species coexistence. *International Journal for Parasitology* , *30* (11), 1147-1152.

Saunders, M.E. and Rader, R., 2019. Network modularity influences plant reproduction in a mosaic tropical agroecosystem. *Proceedings of the Royal Society B* , *286* (1899), 20190296.

Sfair, J.C., Rochelle, A.L., Rezende, A.A., van Melis, J., Weiser, V.D.L. and Martins, F.R., 2015. Weak phylogenetic signal for specialisation in antagonistic liana–tree networks. *Plant Ecology & Diversity* , *8* (3), 379-386.

Sfair, J.C., Rochelle, A.L.C., Rezende, A.A., Van Melis, J., de Lara Weiser, V. and Martins, F.R., 2010. Nested liana-tree network in three distinct neotropical vegetation formations. *Perspectives in Plant Ecology, Evolution and Systematics* , *12* (4), 277-281.

Sfair, J.C., Weiser, V.D.L., Martins, F.R., Vidal, M.M. and Guimaraes Jr, P.R., 2018. Species traits and abundance influence the organization of liana–tree antagonistic interaction. *Austral Ecology* , *43* (2), 236-241.

Silva, I.A., van Melis, J., Sfair, J.C., Martins, F.R. and Ullah, F., 2016. Phylogenetic interactions among lianas in a southeastern Brazilian semideciduous tropical forest. *South African Journal of Botany* , *103* , 108-125.

Staniczenko, P.P., Kopp, J.C. and Allesina, S., 2013. The ghost of nestedness in ecological networks. *Nature communications* , *4* (1), 1-6.

Stone, L. and Roberts, A., 1990. The checkerboard score and species distributions. *Oecologia* , *85* (1), 74-79.

Tang, Y., Kitching, R.L. and Cao, M., 2012. Lianas as structural parasites: a re-evaluation. *Chinese Science Bulletin* , *57* (4), 307-312.

Thebault, E. and Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* , *329* (5993), 853-856.

Thier, O. and Wesenberg, J., 2016. Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro, Brazil. *Tropical Conservation Science* , *9* (2), 852-876.

van Altena, C., Hemerik, L. and de Ruiter, P.C., 2016. Food web stability and weighted connectance: the complexity-stability debate revisited. *Theoretical Ecology* , *9* (1), 49-58.

Vizentin-Bugoni, J., Maruyama, P.K., Debastiani, V.J., Duarte, L.D.S., Dalsgaard, B. and Sazima, M., 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant–hummingbird network. *Journal of Animal Ecology* , *85* (1), 262-272.

Wardhaugh, C.W., Edwards, W. and Stork, N.E., 2015. The specialization and structure of antagonistic and mutualistic networks of beetles on rainforest canopy trees. *Biological journal of the Linnean Society* , *114* (2), 287-295.

Watts, S., Dormann, C. F., Amm, G., Ollerton, J., 2016. The influence of floral traits on specialization and modularity of plant–pollinator networks in a biodiversity hotspot in the Peruvian Andes. *Annals of Botany* , *118* , 415–429.

Wekesa, C., Kirui, B.K., Maranga, E.K., Muturi, G.M. 2019. Variations in forest structure, tree species diversity and above-ground biomass in edges to interior cores of fragmented forest patches of Taita Hills, Kenya. *Forest Ecology and Management* , 440, 48-60.

FIGURE TITLES

FIGURE 1 Individual-based rarefaction-extrapolation curves showing liana species richness patterns in the three forest sites of the two moist semi-deciduous forests in Ghana: (a) Asenanyo Forest Reserve, (b) Suhuma Forest Reserve. The solid lines show the rarefaction (interpolation) curves from the reference sample, while the dashed lines indicate the extrapolation curves. The symbols ending the rarefaction curves (see also legend) represent observed number of individuals for the forest sites.

FIGURE 2 Network modules identified by DIRTLPAwb+ in edge (a), interior (b) and deep-interior (c) sites in Asenanyo Forest Reserve, Ghana. The darker squares represent higher interaction frequency, while the light squares show lower frequency of interaction. The boxes show the modules of the networks, which are consecutively numbered. Each module is made up of liana species on the y-axis and tree species on the x-axis. The species constituting the modules are found in Appendix 2.

FIGURE 3 Network modules identified by DIRTLPAwb+ in edge (a), interior (b) and deep-interior (c) sites in Suhuma Forest Reserve, Ghana. The darker squares represent higher interaction frequency, while the light squares show lower frequency of interaction. The boxes show the modules of the networks, which are consecutively numbered. Each module is made up of liana species on the y-axis and tree species on the x-axis. The species constituting the modules are found in Appendix 2.

FIGURE 4 Module connectivity and interactions plots of the networks that show liana species roles within edge (a), interior (b), and deep-interior (c) forest sites in the Asenanyo Forest Reserve, Ghana. The threshold values of among-module connectivity (c) and within-module interaction (z) which were obtained from 95 % quantiles from 100 null models are denoted by the vertical and horizontal lines. Species names are abbreviated to first two letters of the genus name and at least the first letter of the specific epithet (see appendix 3 for full species names)

FIGURE 5 Module connectivity and interactions plots of the networks that show liana species roles within edge (a), interior (b), and deep-interior (c) forest sites in the Suhuma Forest Reserve, Ghana. The threshold values of among-module connectivity (c) and within-module interaction (z) which were obtained from 95 % quantiles from 100 null models are denoted by the vertical and horizontal lines. Species names are abbreviated to first two letters of the genus name and at least the first letter of the specific epithet (see appendix 3 for full species names)

FIGURE 6 Module connectivity and interactions plots of the networks that show tree species roles within edge (a), interior (b), and deep-interior (c) forest sites in the Asenanyo Forest Reserve, Ghana. The threshold values of among-module connectivity (c) and within-module interaction (z) which were obtained from 95 % quantiles from 100 null models are denoted by the vertical and horizontal lines. Species names are abbreviated to first two letters of the genus name and at least the first letter of the specific epithet (see appendix 4 for full species names)

FIGURE 7 Module connectivity and interactions plots of the networks that show tree species roles within edge (a), interior (b), and deep-interior (c) forest sites in the Suhuma Forest Reserve, Ghana. The threshold values of among-module connectivity (c) and within-module interaction (z) which were obtained from 95 % quantiles from 100 null models are denoted by the vertical and horizontal lines. Species names are abbreviated to first two letters of the genus name and at least the first letter of the specific epithet (see appendix 4 for full species names)

APPENDIX 1 Structure of the three liana-tree networks analysed in edge, interior, and deep-interior forest sites of the Asenanyo (a, b and c, respectively) and Suhuma (d, e and f, respectively) Forest Reserves in Ghana. Each network shows all the observed interactions in the forest management regime. The lower and upper bars represent liana and tree species, respectively. In each network, the bar thickness is proportional to the number of interactions of each species. Species names are abbreviated to first two letters of the genus name and at least the first letter of the specific epithet (refer to Appendices 3 and 4 for full species names).

TABLE 1 Liana species abundance and MEI in the edge and non-edge sites in two moist semi-deciduous forests in Ghana (ES: edge site, IS: interior site, DIS: deep-interior site, MEI: magnitude of edge influence)

ASENANYO SUHUMA

Liana species and families ES IS DIS MEI ES IS DIS MEI

Apocynaceae

Alafia barteri Oliver 40 33 35 0.08 20 16 22 0.03

Alafia sp. 29 13 12 0.40 15 9 9 0.25

Gongronema latifolium Benth. 0 0 0 0 1 0

Landolphia dulcis (Sabine ex G.Don) Pichon 1 0 2 1 4 1

Landolphia hirsuta (Hua) Pichon 0 0 0 9 6 9 0.09

Landolphia owariensis P.Beauv. 0 0 0 0 1 0

Motandra guineensis (Thonn.) A.DC. 39 41 15 0.16 39 22 16 0.34

Oncinotis nitida Benth. 0 0 0 0 0 2

Parquetina nigrescens (Afzel.) Bullock 0 0 0 0 1 0

Strophanthus hirsutus H.Hess 0 0 0 4 0 0

Strophanthus hispidus DC. 1 0 0 0 0 0

Strophanthus preussii Engl. & Pax 8 21 23 -0.52 0 0 0

Strophanthus sarmentosus DC. 0 0 0 6 12 0 0.00

Celastraceae

Hippocratea myriantha Oliv. 0 0 0 0 0 1

Salacia debilis (G.Don) Walp. 3 0 0 2 5 2

Salacia elegans Welw. ex Oliv. 45 43 32 0.09 15 4 20 0.11

Salacia lateritia N.Halle 8 1 0 0 0 0

Salacia leptoclada Tul. 0 0 0 0 3 0

Salacia macrantha A.C.Sm. 0 0 0 0 4 0

Salacia preussii Loes 0 1 0 0 0 0

Salacia cerasifera Welw. Ex Oliv. 0 0 0 0 5 0

Salacia staudtiana Loes. ex Fritsch 0 0 0 0 1 0

Salacighia letestuana (Pellegr.) Blakelock 0 0 0 1 0 0

Simirestis staudtii (Loes.) N.Halle 0 0 0 0 0 2

TABLE 1 (Continued)

ASENANYO SUHUMA

Liana species and families ES IS DIS MEI ES IS DIS MEI

Combretaceae

Combretum acutum M.A.Lawson 0 13 0 -1.00 0 0 0

Combretum comosum G.Don 18 3 21 0.20 0 0 3

Combretum fuscum Planch. ex Benth. 0 0 0 0 0 1

Combretum micranthum G.Don 1 0 0 0 0 0

Combretum mucronatum Schumach. & Thonn. 0 0 0 2 4 5 -0.38

Combretum oyemense Exell 16 3 8 0.49 0 0 0

Combretum paniculatum Vent. 6 14 0 -0.08 7 9 9 -0.13

Combretum smeathmannii G.Don 0 0 0 9 4 7 0.24

Combretum sordidum Exell 0 0 0 2 0 0

Combretum sp. 0 0 0 0 1 0

Combretum tarquense Clark 0 0 0 5 0 16 -0.23

Connaraceae

Agelaea obliqua (P.Beauv.) Baillon 0 2 0 0 0 3

Agelaea trifolia (Lam.) Baill. 1 1 3 1 2 0

Castanola paradoxa (Gilg) Schellenb. 0 0 0 1 0 0

Cnestis ferruginea Vahl ex DC. 0 0 0 0 1 0

Connarus africanus Lam. 0 0 0 0 7 0

Convolvulaceae

Calycobolus africanus (G. Don) Heine 19 23 7 0.12 25 25 23 0.02

Calycobolus heudelotii (Baker ex Oliver) Heine 4 1 0 0 1 1

Neuropeltis acuminata (P.Beauv.) Benth. 8 3 17 -0.11 16 14 12 0.10

Neuropeltis prevosteoides Mangenot 0 0 0 4 4 16 -0.43

Dichapetalaceae

Dichapetalum dewevrei De Wild. & T.Durand 0 0 0 1 0 0

Dichapetalum pallidum (Oliver) Engler 0 1 2 1 0 0

TABLE 1 (Continued)

ASENANYO SUHUMA

Liana species and families ES IS DIS MEI ES IS DIS MEI

Dilleniaceae

Tetracera affinis Hutch. 2 3 1 0 0 0

Euphorbiaceae

Manniophyton fulvum Mull.Arg. 0 3 0 17 6 7 0.45

Hernandiaceae

Illigera pentaphylla Welw. 0 0 0 2 0 1

Icacinaceae

Chlamydocarya macrocarpa A.Chev.exHutch.&D 0 2 0 0 0 0

Lamiaceae

Clerodendrum sp. 0 0 0 1 0 0

Clerodendrum umbellatum Poir 0 0 0 1 0 0

Fabaceae

Acacia kamerunensis Gand. 1 5 2 5 7 15 -0.38

Acacia pentagona (Schum& Thonn.)Hook f. 10 11 9 0.00 14 25 26 -0.29

Baphia capparidifolia Baker 0 0 0 1 0 0

Caesalpinia cucullata Roxb. 12 0 1 0.92 0 0 0

Dalbergia hostilis Bentham 3 3 0 3 1 0

Dalbergia oblongifolia G.Don 0 0 1 0 0 0

Dalbergiella welwitschii (Baker) Baker f. 6 3 5 0.20 3 11 1 -0.33

Griffonia simplicifolia (DC.) Baill. 44 37 50 0.01 63 33 25 0.37

Leptoderris sassandrensis Jongkind 0 0 0 4 2 0

Leptoderris cyclocarpa Dunn 0 0 0 1 0 0

Leptoderris micrantha Dunn 11 3 14 0.13 2 8 1 -0.38

Leptoderris miegei Ake Assi & Mangenot 1 0 0 2 0 8

Leucomphalos libericus Breteler 0 0 0 1 0 0

Mezoneuron benthamianum Baill. 0 0 0 6 0 0

Millettia chrysophylla Dunn 84 74 67 0.09 86 84 44 0.15

Millettia lucens (Scott-Elliot) Dunn 1 0 2 0 0 0

TABLE 1 (Continued)

ASENANYO SUHUMA

Liana species and families ES IS DIS MEI ES IS DIS MEI

Linaceae

Hugonia planchonii Hook.f. 0 0 0 0 1 0

Hugonia rufopilis A.Chev. ex Hutch. & Dalziel 0 0 0 1 0 0

Loganiaceae

Strychnos campicola Gilg 5 8 7 -0.20 0 0 0

Strychnos longicaudata Gilg 0 0 0 9 3 6 0.33

Strychnos malacoclados C.H. Wright 0 0 0 0 3 5

Malpighiaceae

Acridocarpus smeathmannii (DC.) Guill. & Perr. 1 0 0 0 0 0

Grewia hookeriana Exell & Mendonca 1 4 2 0 0 0

Grewia malacocarpa Mast. 0 0 0 7 1 7 0.27

Menispermaceae

Tiliacora dielsiana Hutch. & Dalziel 9 12 12 -0.14 10 5 8 0.21

Triclisia patens Oliv. 1 3 1 0 0 1

Moraceae

Ficus sp. 0 0 0 0 0 2

Phyllantaceae

Phyllanthus sp. 0 0 0 0 0 1

Piperaceae

Piper guineense Shumach. & Thonn. 1 0 0 0 4 1

Polygonaceae

Afrobrunnichia erecta (Asch.) Hutch. & Dalziel 3 2 2 0 0 2

Rubiaceae

Morinda morindoides (Baker) Milne-Redh. 10 8 0 0.43 0 0 0

Mussaenda tristigmatica Cummins 1 0 0 0 0 0

TABLE 1 (Continued)

Liana species ASENANYO SUHUMA

ES IS DIF MEI ES IS DIF MEI

Sapindaceae

Paullinia pinnata Linne 2 15 3 -0.64 0 0 0

Vitaceae

Cissus adenocaulis Steud. ex A.Rich 6 3 1 6 1 1

Cissus silvestris Tchoume 0 1 0 0 0 0

Total number of species 39 36 29 44 41 41

Abundance per 0.25 m^2 plot 58 52 45 54 45 43

TABLE 2 Patterns of network properties of liana-tree interactions among three forest sites of two moist semi-deciduous forests in Ghana

ASENANYO SUHMA

Network metric Observed Null model P-value Observed Null model P-value

Edge

WNODF 11.63 17.82 0.001 6.47 7.51 0.108

Modularity 0.36 0.27 0.001 0.44 0.36 0.001

H2 0.27 0.14 0.001 0.24 0.14 0.001

Connectance 0.13 0.16 0.001 0.06 0.10 0.001

C-score 9.15 9.56 0.013 5.73 5.83 0.281

Interior

WNODF 13.53 18.60 0.001 7.98 8.82 0.233

Modularity 0.41 0.28 0.001 0.42 0.33 0.001

H2 0.32 0.16 0.001 0.23 0.14 0.001

Connectance 0.14 0.18 0.001 0.08 0.10 0.001

C-score 8.90 9.17 0.113 7.04 7.25 0.137

Deep-nterior

WNODF 11.96 16.36 0.008 5.27 5.87 0.229

Modularity 0.41 0.25 0.001 0.45 0.34 0.001

H2 0.33 0.15 0.001 0.24 0.11 0.001

Connectance 0.11 0.15 0.001 0.08 0.13 0.001

C-score 5.83 5.92 0.433 9.16 9.25 0.435

APPENDIX 2 Liana and tree species forming modules in the networks of the forest sites in the two moist semi-deciduous forests in Ghana. Liana species are indicated in **bold** text, while tree species are not bolded. The species are represented by codes, which are made up of first two letters of the genus name and at least the first letter of the specific epithet (see Table 1 for full names of the species).

Module #	**Asenanyo**	**Asenanyo**	**Asenanyo**	**Suhuma**	**Suhuma**	**Suhuma**
	Edge	**Interior**	**Deep-interior**	**Edge**	**Interior**	**Deep-interior**
Module 1	**Cia, Daw, Pig,** Trs	**Cop, Grh, Mog, Stc, Tea, Chm,** Ala, Cep, Dis	**Agt, Mil, Nep, Afe,** Cap, Trd	**Alsp, Caa, Cap, Lao,** Ala, Amp, Buo, Cep, En.an, Ptm, Sck, Coc	**Coa, Cop, Cot, Daw, Grs, Sas,** Cap, Dia, Disp, Fie, Ptm, Str, Ich	**Mog, Daw, Lad,** Dia, Trp
Module 2	**Sad,** Pia	**Agt, Alb, Daw, Grs,** Ena, Gut, Gue, Hec, Tes, Rih	**Ack, Mic,** Alz, Alb, Chp, Nep, Nel, Sck, Trp	**Lah, Mic, Mog,** Alb, Anm, Bap, Bls, Cea, Cep, Cez, Dis, Drp, Mab, Mad, Nep, Trp, Trt	**Ack, Alb, Cnf, Hup, Les, Mic, Tid** Cab, Cog, Lot, Mip, Nav, Rav, Sto, Stp	**Afe, Sas,** Anm, Cop
Module 3	**Mog, Nea, Trp,** Hya, Nep, Nel, Aig	**Caa, Coa, Coo, Dah, Mic, Nea, Tid,** Amp, Cem, Drg, Nep, Pia, Stp	**Alb,** Fua, Ena	**Cls, Cos, Did, Ilp, Les, Nep, Sae, Sts, Nea,** Ant, Ban, Cap, Cea, Cem, Fie, Hak, Heb, Zag, Aig	**Acp, Grm, Pig, Sal,** Bls, Buo, Desp, Mya, Oma, Tua	**Dah, Fisp, Maf, Tid,** Anf, Dak, Dik, Stp
Module 4	**Afe, Grh, Mil, Mut,** Ena, Uac	**Sae, Sal, Sap, Stp, Cia, Trp,** Ban, Be.co, Ce.od, Ch.su, Py.an, Tr.mo	**Acp, Cac, Coo, Lemic, Tea,** Cep, Los, Pia	**Maf, Stl, Tid,** Anp, Mip, Myl, Tei, Trm	**Alsp, Gol, Mog, Sas,** Cep, Cap, Trm, Trp, Trsp	**Cof, Cop, Cot, Sts, Phsp, Cac,** Ban, Dig, Mie, Rih

Module #	**Asenanyo**	**Asenanyo**	**Asenanyo**	**Suhuma**	**Suhuma**	**Suhuma**
Module 5	**Cah, Coo, Cop, Grs, Lad, Sae, Mom,** Cem, Pya, Stt, Trp, Trs, En.ut,	**Ago, Alsp, Maf,** Cea, Etu	**Pap,** Ala	**Agt, Daw, Grm, Hur, Lemie, Sal,** Alf, Bob, Fue, Hya, Rav, Rid	**Lad, Lemic, Nea, Pan, Sae, Stm,** Ban, Cem, Dig, Tra	**Alb** Beo, Dis, Ptm
Module 6	**Acp, Stp,** Pem, Rav	**Acp, Afe, Coc, Pap. Dip,** Hya, Law	**Alsp, Cah, Grs, Mog,** Bec, Ceo, Cog, Irg, Ra.vo	**Dip, Lel, Sth, Lad,** Sck, Zap	**Cac, Com, Cosp, Lah, Sad,** Ala, Buc, Mua	**Caa, Lah, Nea, Cia,** Cem, Pab, Pia, Coc
Module 7	**Ack, Agt, Cac,** Ban	**Lemic, Mom,** Alz, Cog, Cui	**Cia,** Ank	**Cia, Cop, Grs, Lec, Lemic, Nea,** Cas, Dak, Law, Mya, Pae, Str, Stt, Sya, Rih, Enu	**Cah, Lao, Nep,** Pya, Sck, Trt	**Lemic, Stm,** Fua
Module 8	**Sth,** Bap		**Nea, Tid,** Enu, Maa, Sto	**Ack, Acp, Alb, Sad,** Alz, Ansp, Cap, Dia, Muc, Pia, Sto	**Agt, Caa, Cia, Dah, Maf, Stl,** Alf, Amp, Nep, Pia, Coc	**Ilp, Sae, Nep,** Cog, Ena, Hod
Module 9	**Alb, Alsp, Lemie,** Ant, Ceo, Enc, Mip, Zag		**Caa, Daw, Stc,** Cop, Hya, Trm, Trs	**Com, Cos, Cot, Dah,** Tr.sc	**Cos, Sam, Sts,** Bap, Bec, Muc, Myl, Pab	**Onn, Stl,** Tua
Module 10	**Coc,** Irg		**Stp, Dip,** Ban			**Cah, Trp, Com, Grm,** Alz, Cab, Law, Das
Module 11	**Com,** Alz		**Coc, Dao, Lad, Sae, Trp, Grh,** Cem, Elg, Nad, Pya, Stp, Zag			**Ack, Alsp, Lemie,** Amp, Mya, Myl, Pai
Module 12	**Caa, Stc, Acs,** Chs, Fua, Nav, Tet, Rih					**Sad, Cos, Pig,** Bap, Bls, Gut, Sck, Tes
Module 13	**Dah, Lemic, Mic, Sth,** Ala, Bec, Fis, Stp, Los					**Him, Coc,** Trm

Module #	**Asenanyo**	**Asenanyo**	**Asenanyo**	**Suhuma**	**Suhuma**	**Suhuma**
Module 14	**Pap, Sal, Tea, Tid** Con, Desp					**Acp, Grs, Mic** Ant, Cap, Hya, Irg, Nep, Pesp, Pya, Trsp

APPENDIX 3 Standardised specialisation index (*d’*) for liana species within liana-tree networks in three forest sites of two moist semi-deciduous forests, Ghana. Values with an asterisk are significantly higher than expected by chance.

Liana species ASENANYO SUHUMA

Edge Interior Deep-interior Edge Interior Deep-interior

Acacia kamerunensis Gand. 0.41* - 0.64* 0.30 0.45* 0.39*

Acacia pentagona (Schum& Thonn.) Hook f. 0.47* 0.34* 0.54* 0.55* 0.65* 0.32

Acridocarpus smeathmannii (DC.) Guill. & Perr. 0.66* - - - - -

Afrobrunnichia erecta (Asch.) Hutch. & Dalziel 0.63* 0.59* - - - -

Agelaea obliqua (P.Beauv.) Baillon - 0.40* - - - 0.17

Agelaea trifolia (Lam.) Baill. 0.27 0.60* 1.00* 0.80* 0.48*

Alafia barteri Oliver 0.18 0.28 0.29 0.54* 0.38 0.42*

Alafia sp. 0.39* 0.30 0.30 0.43* 0.13 0.17

Caesalpinia cucullata Roxb. 0.27 - 0.31 - 0.31 -

Calycobolus africanus (G. Don) Heine 0.16 0.22 0.56* 0.25 0.13 0.21

Calycobolus heudelotii (Baker ex Oliver) Heine 0.36* - 0.00 - 1.00* 0.69*

Castanola paradoxa (Gilg) Schellenb. - - - 0.43* - -

Chlamydocarya macrocarpa A.Chev.exHutch.&D - 0.54* - - - -

Cissus adenocaulis Steud. ex A.Rich 0.12 0.67* 0.58* 0.23 0.19 0.00

Cissus silvestris Tchoume - 0.72* - - - -

Clerodendrum sp. - - - 0.30 - -

Cnestis ferruginea Vahl ex DC. - - - - 0.31 -

Combretum acutum M.A.Lawson - 0.53* - - - -

Combretum comosum G.Don 0.31 0.13 0.44* - - 0.71*

Combretum fuscum Planch. ex Benth. - - - - - 0.41*

Combretum micranthum G.Don 0.66* - - - - -

Combretum mucronatum Schumach. & Thonn. - - - 0.39* 0.03 0.42*

Combretum oyemense Exell 0.33* 0.08 0.45* - - -

Combretum paniculatum Vent. 0.34* 0.54* - 0.48* 0.24 0.43*

Combretum smeathmannii G.Don - - - 0.14 0.87* 0.44*

APPENDIX 3 (Continued)

Liana species ASENANYO SUHUMA

Edge Interior Deep-interior Edge Interior Deep-interior

Combretum sordidum Exell - - - 0.55* - -

Combretum sp. - - - - 0.31 -

Combretum tarquense Clark - - - 0.19 0.62* 0.22

Connarus africanus Lam. - - - - 0.64* -

Dalbergia hostilis Bentham 0.43* 0.13 - 0.25 1.00* -

Dalbergia oblongifolia G.Don - - 0.09 - - -

Dalbergiella welwitschii (Baker) Baker f. 0.32* 0.30 0.52* 0.35 0.13 0.49*

Dichapetalum dewevrei De Wild. & T.Durand - - - 0.60* - -

Dichapetalum pallidum (Oliver) Engler - 0.34* 0.59* 0.53* - -

Ficus sp. - - - - - 0.42*

Gongronema latifolium Benth. - - - - 0.44* -

Grewia hookeriana Exell & Mendonca 0.66* 0.24 0.81* - - -

Grewia malacocarpa Mast. - - - 0.45* 0.52* 0.56*

Griffonia simplicifolia (DC.) Baill. 0.11 0.28 0.24 0.26 0.17 0.40*

Hippocratea myriantha Oliv. - - - - - 0.45*

Hugonia planchonii Hook.f. - - - - 0.63* -

Hugonia rufopilis A.Chev. ex Hutch. & Dalziel - - - 0.53* - -

Illigera pentaphylla Welw. - - - 1.00* - 0.45*

Landolphia dulcis (Sabine ex G.Don) Pichon 0.22 - 0.24 0.43* 0.00 0.49*

Landolphia hirsuta (Hua) Pichon - - - 0.08 0.34 0.26

Landolphia owariensis P.Beauv. - - - 0.80* 0.81* -

Leptoderris cyclocarpa Dunn - - - 0.09 - -

Leptoderris micrantha Dunn 0.62* 0.54* 0.54* 0.68* 0.08 0.68*

Leptoderris miegei Ake Assi & Mangenot 0.11 - - 0.43* - 0.47*

Leptoderris sassandrensis Jongkind - - - 0.30 0.38 -

Leucomphalos libericus Breteler - - - 0.53* - -

APPENDIX 3 (Continued)

Liana species ASENANYO SUHUMA

Edge Interior Deep-interior Edge Interior Deep-interior

Manniophyton fulvum Mull.Arg. - 0.82* - 0.62* 0.38 0.36

Millettia chrysophylla Dunn 0.25 0.28 0.35* 0.35 0.16 0.34

Millettia lucens (Scott-Elliot) Dunn 0.75* - 0.59* - - -

Morinda morindoides (Baker) Milne-Redh. 0.21 0.59* - - - -

Mezoneuron benthamianum Baill. - ‘ - - 0.26 - -

Motandra guineensis (Thonn.) A.DC. 0.20 0.20 0.26 0.45* 0.22 0.32

Mussaenda tristigmatica Cummins 0.66* - - - - -

Neuropeltis acuminata (P.Beauv.) Benth. 0.26 0.45* 0.44* 0.47* 0.28 0.33

Neuropeltis prevosteoides Mangenot - - 0.43* 0.29 0.63* 0.27

Oncinotis nitida Benth. - - - - - 0.35

Parquetina nigrescens (Afzel.) Bullock - - - - 0.00 -

Paullinia pinnata Linne 0.52* 0.43* 0.85* - - -

Phyllanthus sp. - - - - - 0.41*

Piper guineense Shumach. & Thonn. 0.29 - - - 0.46* 0.80*

Salacia cerasifera Welw. Ex Oliv. - - - - 0.37 -

Salacia debilis (G.Don) Walp. 0.92* - - 0.53* 0.33 0.48*

Salacia elegans Welw. ex Oliv. 0.24 0.31 0.23 0.23 0.18 0.38*

Salacia lateritia N.Halle 0.67* 0.16 - - - -

Salacia leptoclada Tul. - - - - 0.69* -

Salacia macrantha A.C.Sm. - - - - 0.63* -

Salacia preussii Loes - 0.45* - - - -

Salacia staudtiana Loes. ex Fritsch - - - - 0.81* -

Salacighia letestuana (Pellegr.) Blakelock - - - 0.69* - -

Simirestis staudtii (Loes.) N.Halle - - - - - 0.63*

Strophanthus hirsutus H.Hess - - - 0.61* - -

Strophanthus hispidus DC. 0.73* - - - - -

APPENDIX 3 (Continued)

Liana species ASENANYO SUHUMA

Edge Interior Deep-interior Edge Interior Deep-interior

Strophanthus preussii Engl. & Pax 0.37* 0.19 0.16 - - -

Strophanthus sarmentosus DC. - - - 0.30 0.70* 0.35

Strychnos campicola Gilg 0.51* 0.42* 0.59* - - -

Strychnos longicaudata Gilg - - - 0.34 0.40 0.50*

Strychnos malacoclados C.H. Wright - - - - 0.10 0.48*

Tetracera affinis Hutch. 0.52* 0.40* 0.42* - - -

Tiliacora dielsiana Hutch. & Dalziel 0.38* 0.26 0.44* 0.38* 0.49* 0.49*

Triclisia patens Oliv. 0.83* 0.53* 0.29 - - 1.00*

APPENDIX 4 Standardised specialisation index (*d'*) for tree species within liana-tree networks in three forest sites of two moist semi-deciduous forests, Ghana. Values with an asterisk are significantly higher than expected by chance.

ASENANYO SUHUMA

Tree species Edge Interior Deep-interior Edge Interior Deep-interior

Aidia genipiflora 0.16 - - 1.00* - -

Albizia adianthifolia 0.39* 0.20 0.17 0.23 0.37* -

Albizia ferruginea - - - 0.63* 0.22 -

Albizia zygia 0.00 0.36* 0.18 0.52* - 0.29

Alstonia boonei - - 0.13 0.49* - -

Amphimas pterocarpoides - 0.55* - 0.30 1.00* 0.39*

Annickia polycarpa - - - 0.42* - -

Anopyxis klaineana - - 0.07 - - -

Anthocleista sp. - - - 0.28 - -

Anthonotha fragrans - - - - - 0.41*

Anthonotha macrophylla - - - 0.00 - -

Antiaris toxicaria 0.11 - - 0.37 - 0.15

Antrocaryon micraster - - - - - 0.37*

Baphia nitida 0.29 0.10 0.39* 0.34 0.15 0.28

Baphia pubescens 0.16 - - 0.25 0.69* 0.12

Berlinia confusa 0.12 0.33* 0.09 - 0.54* -

Berlinia occidentalis - - - - - 0.41*

Blighia sapida - - - 0.15 0.39* 0.27

Bombax buonopozense - - - 0.34 - -

Buchholzia coriacea - - - - 0.32 -

Bussea occidentalis - - - 0.26 0.82* -

Calpocalyx brevibracteatus - - - 0.27 0.18 0.33

Carapa procera - - 0.42* 0.28 0.65* 0.31

Canarium schweinfurtii - - - 0.21 - -

Cedrela odorata 0.33* 0.19 0.24 0.00 - -

APPENDIX 4 (Continued)

ASENANYO SUHUMA

Tree species Edge Interior Deep-interior Edge Interior Deep-interior

Ceiba pentandra - 0.43* 0.65* 0.17 0.14 -

Celtis adolfi-friderici - 0.50* - 0.24 - -

Celtis mildbraedii 0.16 0.27 0.29 0.18 0.14 0.17

Celtis philippensis Blanco - - - 0.12 - -

Celtis zenkeri - - - 0.11 - -

Chrysophyllum perpulchrum - - 0.42* - - -

Chrysophyllum subnudum 0.48* 0.38* - - - -

Cola chlamydantha - - - 0.34 0.46* 0.12

Cola gigantea - 0.46* 0.09 - 0.37* 0.52*

Cola nitida 0.14 - - - - -

Corynanthe pachyceras - - 0.66* - 0.08 0.23

Cuviera nigrescens - 0.34* - - - -

Dacryodes klaineana - - - 0.80* - 0.41*

Daniela sp. - - - - - 0.31

Desplatsia sp. 0.73* - - - 0.39* -

Dialium aubrevillei - - - 0.37 0.20 0.45*

Diospyros sanza-minika - - - 0.28 - 0.41*

Diospyros gabunensis - - - - 0.32 0.71*

Diospyros kamerunensis - - - - - 0.60*

Discoglypremna sp. - 0.17 - - - -

Distemonanthus sp. - - - - 0.65* -

Drypetes gilgiana - 0.11 - - - -

Drypetes principum - - - 0.21 - -

Elaeis guineensis Jacq. - - 0.25 - - -

APPENDIX 4 (Continued)

ASENANYO SUHUMA

Tree species Edge Interior Deep-interior Edge Interior Deep-interior

Entandrophragma angolense 0.94* 0.22 0.38* 0.16 - 0.33

Entandrophragma cylindricum 0.23 - - - - -

Entandrophragma utile 0.21 0.89* 0.25 0.27 - -

Ficus exasperata - - - 0.34 0.18 -

Ficus sur 0.51* - - - - -

Funtumia africana 0.09 - 0.37* - - 0.64*

Funtumia elastica - - - 0.60* - -

Guarea thompsonii	-	0.30	-	-	-	0.31
Guibourtia ehie	-	0.11	-	-	-	-
Hannoa klaineana	-	-	-	0.37*	-	-
Hevea brasiliensis	-	-	-	0.23	-	-
Hexalobus crispiflorus	-	0.27	-	-	-	-
Homalium dewevrei	-	-	-	-	-	0.40*
Hymenostegia afzelii	0.22	0.26	0.77*	0.28	-	0.23
Irvingia gabonensis	0.45*	-	0.28	-	-	0.32
Lannea welwitschii	-	0.59*	-	0.38*	-	1.00*
Lonchocarpus sericeus	0.37*	-	0.30	-	-	-
Lovoa trichilioides	-	-	-	-	0.24	-
Macaranga barteri	-	-	-	0.00	-	-
Mammea africana	-	-	0.55*	-	-	-
Margaritaria discoidea	-	-	-	0.64*	-	-
Microdesmis puberula	0.22	-	-	0.19	0.18	-
Milicia excelsa	-	-	-	-	-	0.40*
Musanga cecropioides	-	-	-	0.42*	0.38*	-
Massularia acuminata	-	-	-	-	0.25	-

APPENDIX 4 (Continued)

ASENANYO SUHUMA

Tree species	Edge	Interior	Deep-interior	Edge	Interior	Deep-interior
Myrianthus arboreus	-	-	-	0.43*	0.56*	0.54*
Myrianthus libericus	-	-	-	0.20	0.36	0.40*
Napoleonaea vogelii	0.31*	-	-	-	0.18	-
Nauclea diderrichii	-	-	0.25	-	-	-
Nesogordonia papaverifera	0.26	0.00	0.16	0.22	0.30	0.25
Newbouldia laevis	0.56*	-	0.00	-	-	-
Omphalocarpum ahia	-	-	-	-	0.39	-
Pachystela msolo	-	-	-	-	-	0.54*
Pachystela brevipes	-	-	-	-	0.00	-
Parinari excelsa	-	-	-	0.32	-	-
Parkia bicolor	-	-	-	-	-	0.37*
Pentaclethra sp.	-	-	-	-	-	0.00
Petersianthus macrocarpus	0.53*	-	-	-	-	-

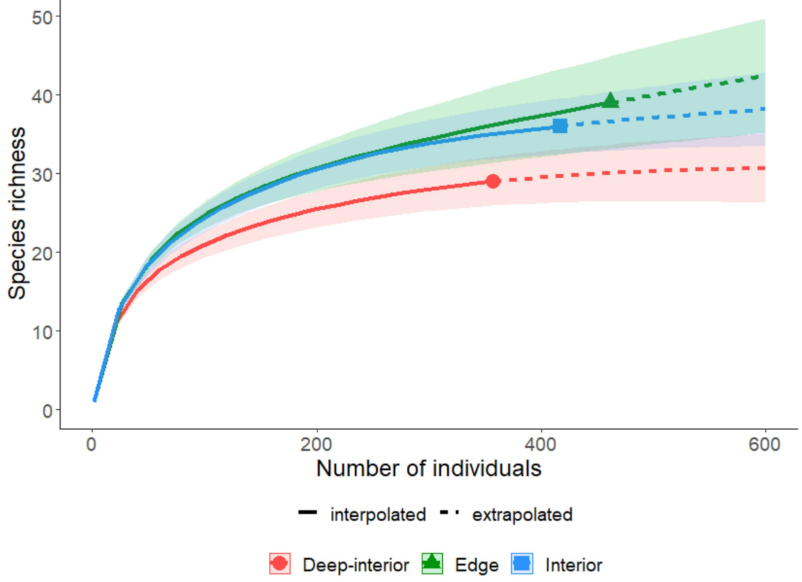
Piptadeniastrum africanum	0.87*	0.19	0.45*	0.46*	0.41*	0.23
Pterygota macrocarpa	-	-	-	0.58*	0.29	0.20
Pycnanthus angolensis	0.72*	0.39*	0.49*	-	0.35	0.23
Rauvolfia vomitoria	0.63*	-	0.21	0.59*	0.37*	-
Ricinodendron heudelotii	0.54*	0.47*	-	0.22	0.26	0.28
Rinorea sp.	-	-	-	0.86*	-	-
Scottellia klaineana	-	-	0.18	0.33	1.00*	0.69*
Sterculia oblonga	-	-	0.49*	0.37*	0.29	-
Sterculia rhinopetala	-	-	-	0.16	0.05	-
Sterculia tragacantha	0.13	-	-	0.23	-	-
Strombosia pustulata	0.18	0.22	0.23	0.79*	0.09	0.28
Synsepalum aubrevillei	-	-	-	0.00	-	-

APPENDIX 4 (Continued)

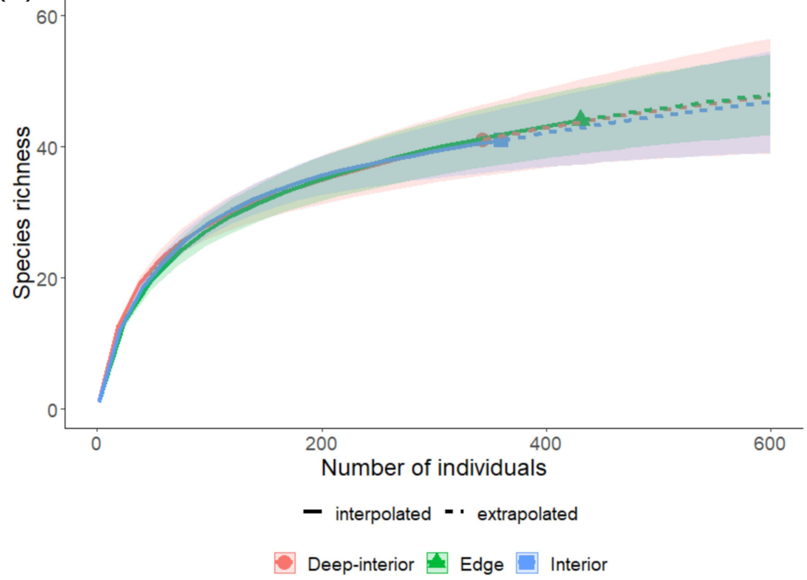
ASENANYO SUHUMA

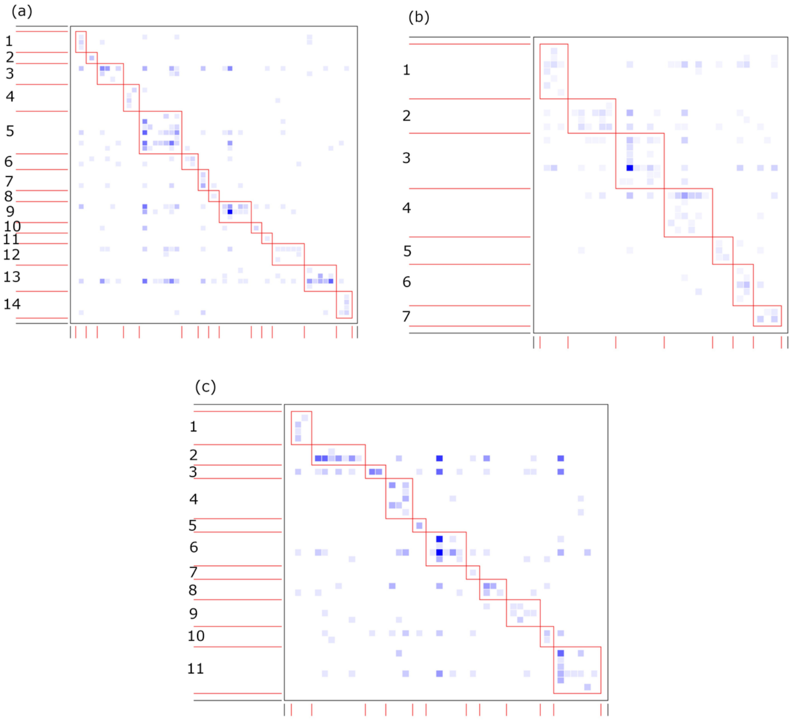
Tree species	Edge	Interior	Deep-interior	Edge	Interior	Deep-interior
Terminalia ivorensis	-	-	-	0.58*	-	-
Terminalia superba	-	0.17	-	-	-	0.43*
Tetrapleura tetraptera	0.10	-	-	-	-	-
Treculia africana	-	-	-	-	0.07	-
Trichilia monadelpha	0.12	0.11	0.29	0.41*	0.35	0.31
Trichilia prieuriana	0.23	-	0.00	0.11	0.20	0.17
Trichilia tessmannii	-	-	-	-	0.37*	-
Tricalysia disco lor	-	-	1.00*	-	-	-
Trilepisium sp.	0.18	-	-	0.12	0.45*	0.00
Triplochiton scleroxylon	0.10	-	0.22	0.55*	-	-
Turraeanthus africanus	-	-	-	-	0.34	0.40*
Uapaca corbisieri	0.90*	-	-	-	-	-
Zanthoxylum gilletii	0.13	-	0.25	0.38*	-	-
Zanthoxylum parvifoliolum	-	-	-	0.78*	-	-

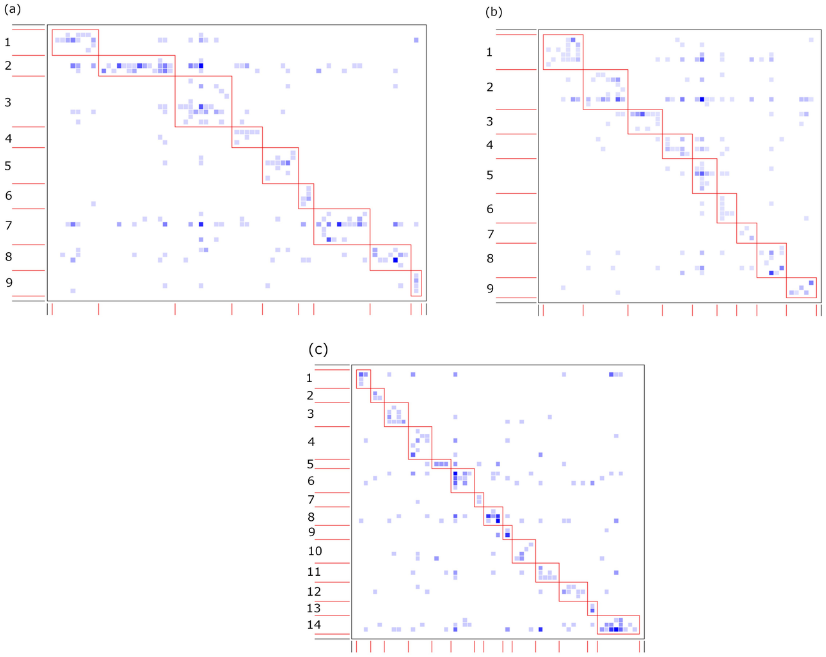
(a)

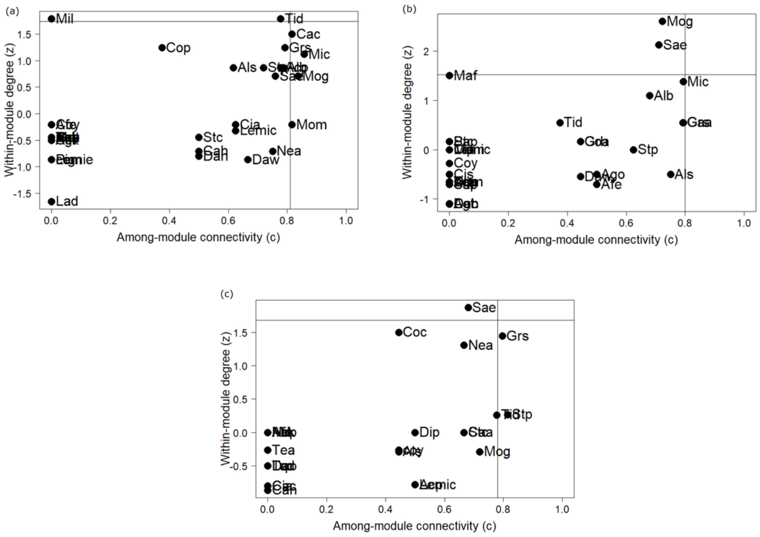

Species richness
0
10
20
30
40
50
0
200
400
600
Number of individuals
interpolated
extrapolated
Deep-interior
Edge
Interior

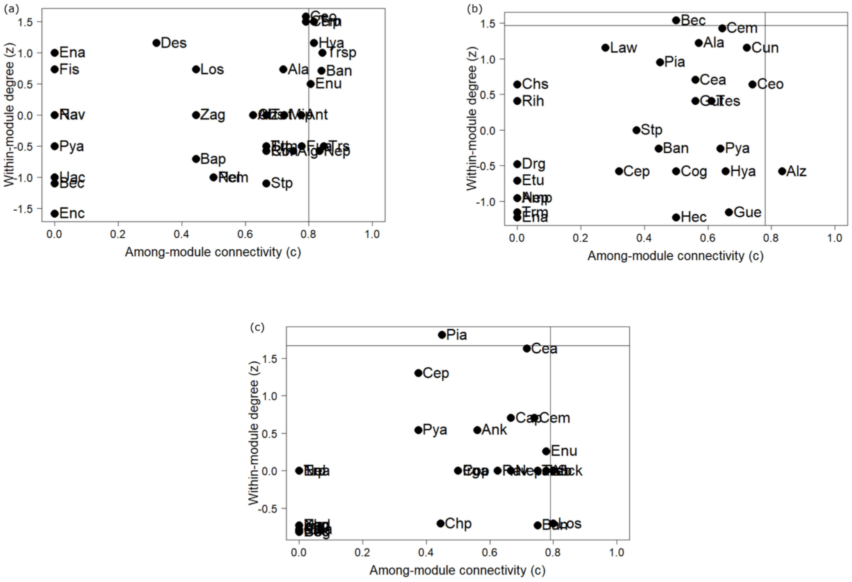
(b)

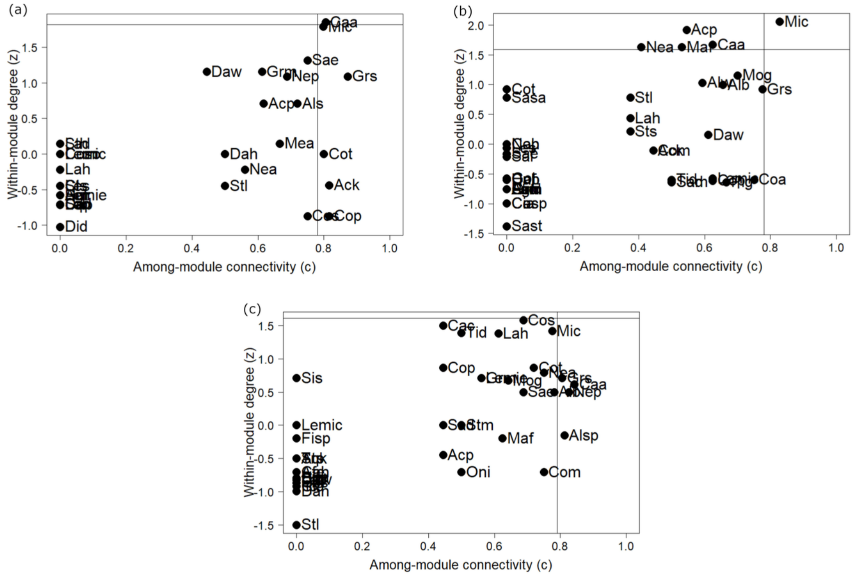

Species richness
0
20
40
60
0
200
400
600
Number of individuals
interpolated
extrapolated
Deep-interior
Edge
Interior

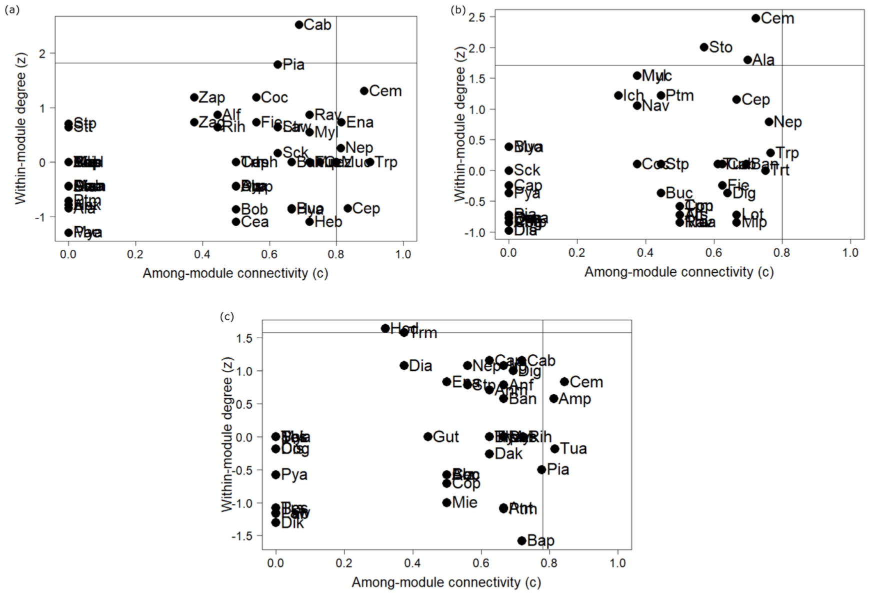

(a)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
(b)
1
2
3
4
5
6
7
(c)
1
2
3
4
5
6
7
8
9
10
11


(a)
1
2
3
4
5
6
7
8
9
(b)
1
2
3
4
5
6
7
8
9
(c)
1
2
3
4
5
6
7
8
9
10
11
12
13
14

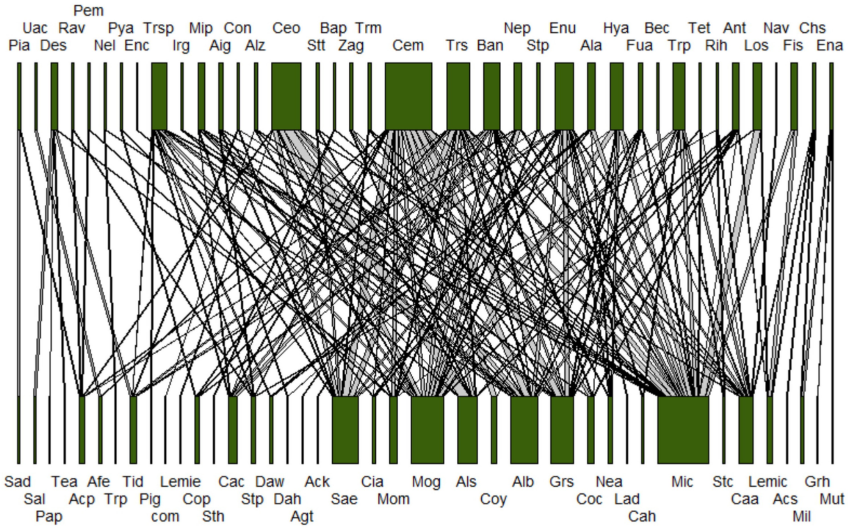

(a)
Within-module degree (z)
Among-module connectivity (c)
Mil
Tid
Cac
Cop
Grs
Mic
Als
Sae
Mog
Cia
Lemic
Mom
Stc
Cah
Dan
Nea
Daw
Lad
(b)
Mog
Sae
Maf
Mic
Alb
Tid
Gda
Stp
Coy
Cis
Ago
Afe
Als
(c)
Sae
Coc
Grs
Nea
Dip
Sta
Mog
Tea
Lemic


(a)
Within-module degree (z)
Among-module connectivity (c)
Ceo
Cem
Des
Hya
Trsp
Ena
Fis
Los
Ala
Ban
Enu
Rav
Zag
Ant
Pya
Trs
Nep
Bap
Rem
Hac
Bec
Stp
Enc
(b)
Bec
Cem
Ala
Law
Cun
Pia
Cea
Ceo
Chs
Rih
Tes
Stp
Ban
Pya
Drg
Cep
Cog
Hya
Alz
Etu
Hec
Gue
Ena
(c)
Pia
Cea
Cep
Cap
Cem
Pya
Ank
Enu
Chp
Los

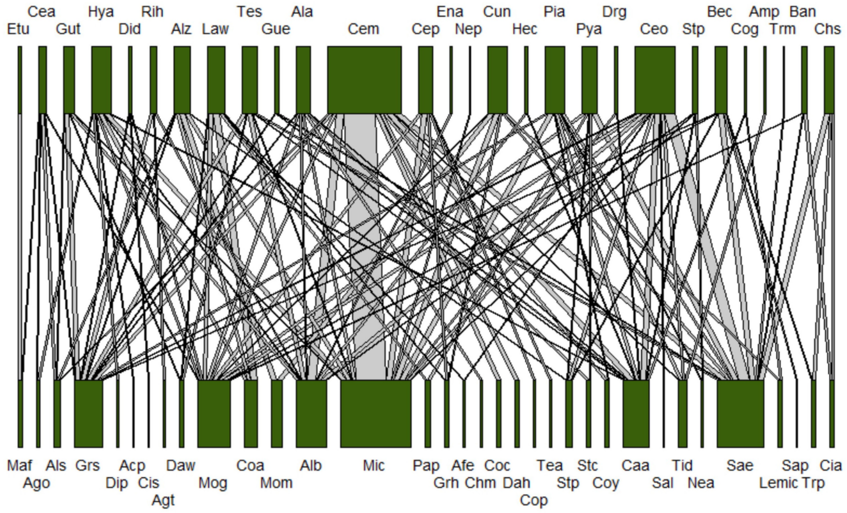

(a)
(b)
(c)
Within-module degree (z)
Among-module connectivity (c)
Caa
Mic
Sae
Daw
Grm
Nep
Grs
Acp
Als
Mea
Dah
Cot
Nea
Stl
Ack
Cop
Lah
Did
Acp
Nea
Maf
Mog
Alb
Stl
Lah
Sts
Daw
Com
Coa
Sasa
Sast
Cos
Cac
Tid
Sis
Lemic
Fisp
Maf
Alsp
Oni
Stm
Stl
Dan


(a)
(b)
(c)
Within-module degree (z)
Among-module connectivity (c)
Cab
Pia
Cem
Zap
Coc
Alf
Rih
Rav
Ena
Myl
Sck
Nep
Trp
Bob
Cea
Heb
Cep
Pya
Cem
Sto
Ala
Ich
Ptm
Nav
Cep
Nep
Trp
Trt
Stp
Buc
Dig
Lot
Mip
Hed
Trm
Dia
Cab
Dig
Anf
Ban
Amp
Gut
Dak
Tua
Pia
Cop
Mie
Bap
Dik

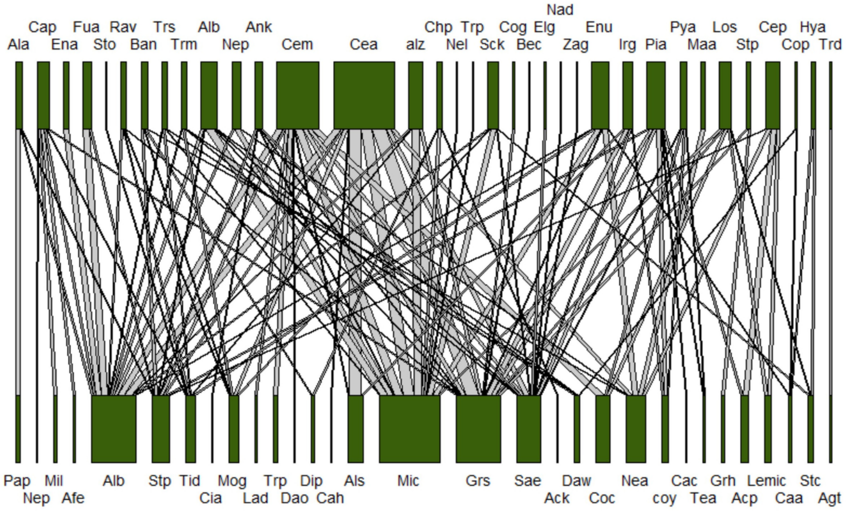
(a)


Pem
Uac Rav Pya Trsp Mip Con Ceo Bap Trm Nep Enu Hya Bec Tet Ant Nav Chs
Pia Des Nel Enc Irg Aig Alz Stt Zag Cem Trs Ban Stp Ala Fua Trp Rih Los Fis Ena
Sad Tea Afe Tid Lemie Cac Daw Ack Cia Mog Als Alb Grs Nea Mic Stc Lemic Grh
Sal Acp Trp Pig Cop Stp Dah Sae Mom Coy Coc Lad Caa Acs Mut
Pap com Sth Agt Cah Mil

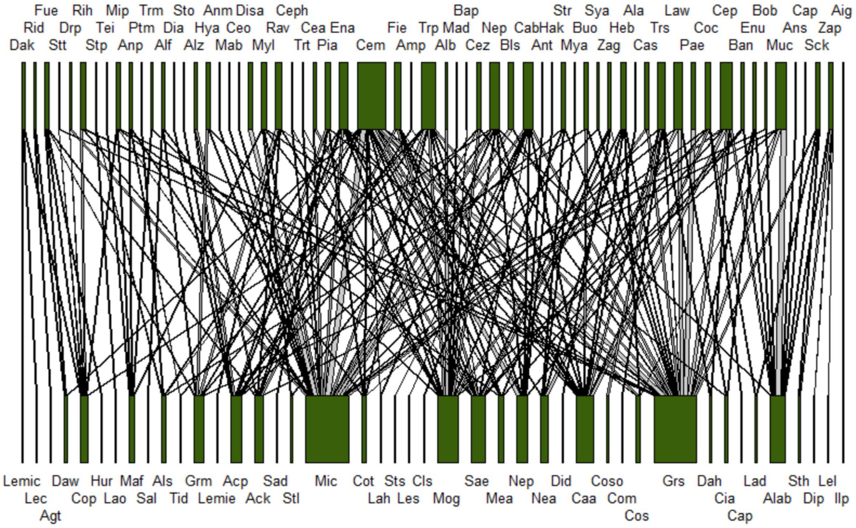
(b)


Cea Hya Rih Tes Ala Ena Cun Pia Drg Bec Amp Ban
Etu Gut Did Alz Law Gue Cem Cep Nep Hec Pya Ceo Stp Cog Trm Chs
Maf Als Grs Acp Daw Coa Alb Mic Pap Afe Coc Tea Stc Caa Tid Sae Sap Cia
Ago Dip Cis Mog Mom Grh Chm Dah Stp Coy Sal Nea Lemic Trp
Agt Cop

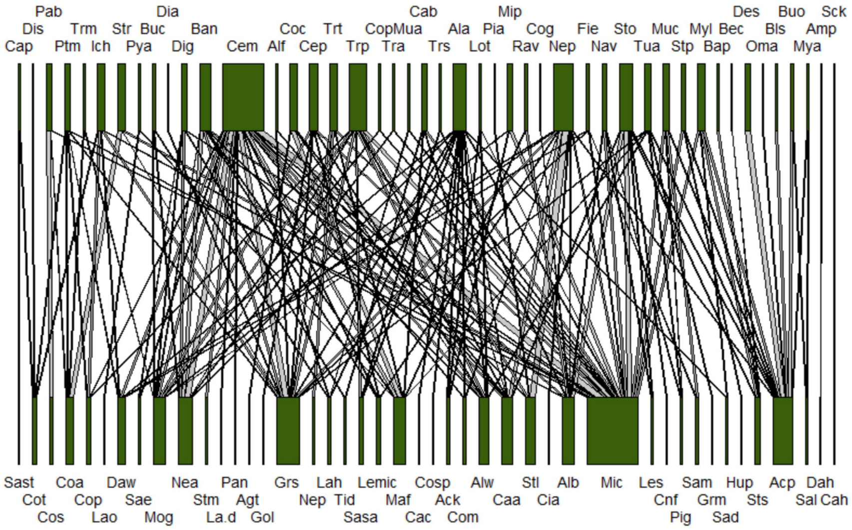
(c)


Nad
Cap
Fua
Rav
Trs
Alb
Ank
Chp
Trp
Cog
Elg
Enu
Pya
Los
Cep
Hya
Ala
Ena
Sto
Ban
Trm
Nep
Cem
Cea
alz
Nel
Sck
Bec
Zag
Irg
Pia
Maa
Stp
Cop
Trd
Pap
Mil
Alb
Stp
Tid
Mog
Trp
Dip
Als
Mic
Grs
Sae
Daw
Nea
Cac
Grh
Lemic
Stc
Nep
Afe
Cia
Lad
Dao
Cah
Ack
Coc
coy
Tea
Acp
Caa
Agt

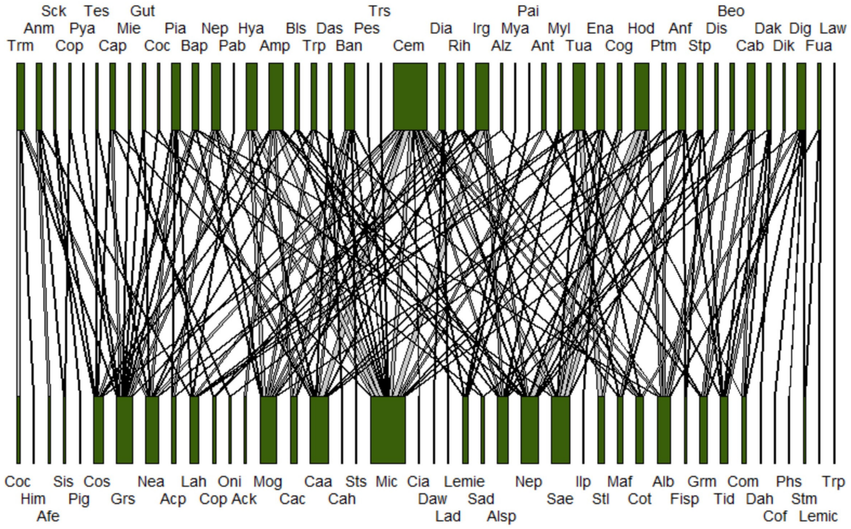
(d)


Fue
Rih
Mip
Trm
Sto
Anm
Disa
Ceph
Bap
Str
Sya
Ala
Law
Cep
Bob
Cap
Aig
Rid
Drp
Tei
Ptm
Dia
Hya
Ceo
Rav
Cea
Ena
Fie
Trp
Mad
Nep
Cab
Hak
Buo
Heb
Trs
Coc
Enu
Ans
Zap
Dak
Stt
Stp
Amp
Alf
Alz
Mab
Myl
Trt
Pia
Cem
Amp
Alb
Cez
Bls
Ant
Mya
Zag
Cas
Pae
Ban
Muc
Sck
Lemic
Daw
Hur
Maf
Als
Grm
Acp
Sad
Mic
Cot
Sts
Cls
Sae
Nep
Did
Coso
Grs
Dah
Lad
Sth
Lel
Lec
Cop
Lao
Sal
Tid
Lemie
Ack
Stl
Lah
Les
Mog
Mea
Nea
Caa
Com
Cia
Alab
Dip
Ilp
Agt
Cos
Cap

(e)


Pab Dia Cab Mip Des Buo Sck
Dis Trm Str Buc Ban Coc Trt CopMua Ala Pia Cog Fie Sto Muc Myl Bec Bls Amp
Cap Ptm Ich Pya Dig Cem Alf Cep Trp Tra Trs Lot Rav Nep Nav Tua Stp Bap Oma Mya
Sast Coa Daw Nea Pan Grs Lah Lemic Cosp Alw Stl Alb Mic Les Sam Hup Acp Dah
Cot Cop Sae Stm Agt Nep Tid Maf Ack Caa Cia Cnf Grm Sts Sal Cah
Cos Lao Mog La.d Gol Sasa Cac Com Pig Sad

(f)


Sck Tes Gut Trs Pai Beo
Anm Pya Mie Pia Nep Hya Bls Das Pes Dia Irg Mya Myl Ena Hod Anf Dis Dak Dig Law
Trm Cop Cap Coc Bap Pab Amp Trp Ban Cem Rih Alz Ant Tua Cog Ptm Stp Cab Dik Fua
Coc Sis Cos Nea Lah Oni Mog Caa Sts Mic Cia Lemie Nep Ilp Maf Alb Grm Com Phs Trp
Him Pig Grs Acp Cop Ack Cac Cah Daw Sad Sae Stl Cot Fisp Tid Dah Stm
Afe Lad Alsp Cof Lemic