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Calibrating the liana crown occupancy index in Amazonian forests

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ABSTRACT

Lianas hold an important, but understudied, role in forest dynamics, however they are difficult to measure and detailed liana measurements are time consuming. Many researchers have therefore used an ordinal scale index, the crown occupancy index (COI), to describe the liana load carried by trees. Here we assess the overall effectiveness, in terms of accuracy, precision, repeatability and efficiency, of the COI in tropical forests. We relate the COI to more detailed liana measurements at the individual tree-level and site-level, comparing sites with different levels of liana infestation. Our results show (1) that the COI accurately measures individual tree and plot level liana loads, indicated by the strong correlations between the COI and the number and basal area of lianas. However, (2) as expected, the COI is only weakly related to the basal area of lianas rooted close to the tree, which is a proxy for competition for below-ground resources. The COI is also (3) an efficient measure of liana loads, as the input time needed for a COI survey is considerably less than that of a detailed liana survey. We also (4) found a high degree of repeatability in COI classification between observers. Additionally (5), the COI can be used to differentiate between sites in terms of their overall liana canopy competition (precision), but (6) may not be a precise indicator of the site-level mean basal area of lianas in tree crowns.

1. Introduction

Lianas (woody climbing plants) are an abundant and dynamic component of tropical forests. They rely on other plants for structural support and as such can increase tree mortality risks (Putz, 1984; Phillips et al., 2005), reduce tree growth (Putz, 1984; Clark and Clark, 1990; van der Heijden and Phillips, 2009a) and fecundity (Stevens, 1987; Kainer et al., 2006; Fonseca et al., 2009), affect tree regeneration (Schnitzer et al., 2000) and cause trunk and stem deformations (Putz, 1991). We might expect that the magnitude of these effects will differ depending on the liana load a host tree carries, and indeed some studies have shown that more heavily infested trees are more severely affected by lianas than lightly infested trees in both tropical (e.g. van der Heijden and Phillips, 2009a) and temperate forests (e.g., Ladwig and Meiners, 2009). Being able to reliably assess liana infestation loads is therefore important both for foresters and ecologists to help, for example, (1) assess whether extracting timber leads to increased infestation of residual stand and regrowth; (2) compare the impact of different management techniques on liana infestation; (3) determine the impact of liana loads on commercial fruit production; (4) test hypotheses of change in liana loads over time; and (5) compare liana infestation patterns across sites.

However, lianas are notoriously difficult to measure and detailed liana measurements can be time consuming. Many tropical foresters and ecologists have therefore sought short-cuts to describing the liana load carried by trees by using simple ordinal scale indices. Foremost amongst these is the "crown occupancy index" (COI) (Clark and Clark, 1990), which expresses liana loads in the tree crown on a five-point scale: (0) no lianas in the crown, (1) 1–25%, (2) 26–50%, (3) 51–75%, and (4) >75% of the tree crown covered by liana leaves. This index and similar 3- or 4-category variations are now widely used in liana research (e.g., Gerwing, 2001; O'Brien et al., 2004; Rice et al., 2004; Wadt et al., 2005; Wright et al., 2005; Kainer et al., 2006, 2007; Fonseca et al., 2009; Grogan and Landis, 2009; Ladwig and Meiners, 2009). However, whilst this categorical division to classify liana infestation loads is increasingly used, so far the overall effectiveness of the COI has yet to be assessed. The value of the use of the COI depends on the extent we can have confidence in the accuracy, precision, repeatability and efficiency with which it can be applied to the forest environment.

To this end, the aims of this study are to (1) evaluate the strength of the correlation between the COI and detailed liana measurements both for individual tree and stand-levels (*accuracy*), (2) test whether the COI can be used to discriminate between differences

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in liana infestation within and between sites (*precision*), (3) assess inter-observer bias in using the COI (*repeatability*), and (4) to compare input time between a detailed liana survey and a COI survey (*efficiency*).

2. Methods

2.1. Data collection

We worked in three sites across Amazonia: Nouragues (French Guyana;) in the north-east (4°4′60.0″N, 52° 40′0.1″W); Tambopata Nature Reserve (Peru) in the south-west (12°50′5.1″S, 69°17′9.9″W), and Noel Kempff (Bolivia) in the south (Huanchaca 14°31′45.4″S, 60°43′59.3″W and Los Fierros 14°34′39.0″S, 60°49′55.0″W). These sites lie in distinct floristic zones (ter Steege et al., 2006; Honorio Conorado et al., 2009), which can lead to differences both in liana-host relationships and liana dominance (van der Heijden et al., 2008; van der Heijden and Phillips, 2009a), and so are expected to provide a suitable range of conditions for comparing the effectiveness of the COI. See Malhi et al. (2002) for further description of the sites.

At Nouragues, we surveyed nineteen 50 m × 50 m plots, totalling 1641 trees ≥10 cm diameter at breast height (dbh) located in mature lowland tropical forest of the Grand Plateau. In Tambopata and Noel Kempff only subsets of trees in 1-ha plots were sampled: a random subset of 386 trees ≥10 cm dbh in three 1-ha plots in Tambopata and 178 trees ≥10 cm dbh following a stratified design in four 1-ha plots in Noel Kempff.

In each of the three sites, the liana load of trees ≥10 cm (dbh) was classified (1) using the COI based upon the five-category system of Clark and Clark (1990), and (2) with detailed liana measurements. In Nouragues and Tambopata, each tree was assigned a COI value by at least two independent observers; in Noel Kempff, only one observer was used.

The detailed liana measurements differed slightly between sites. At Nouragues and Tambopata, the diameter at 1.3 m from the last rooting point (*cf.* Gerwing et al., 2006) was measured for lianas >1.3 m long growing in proximity to the subject tree, or estimated in 1 cm size-classes at the point where they entered the tree crown when direct measurement was not possible. As lianas sometimes climb from tree crown to tree crown (e.g., Putz, 1984), their leaf area and biomass may be spread over more than one tree. Therefore, to avoid possible double-counting of liana impact on trees, we also estimated the diameter of liana stems growing out of the tree crown in 1 cm size-classes at their point of exit from the crown (*cf.* van der Heijden and Phillips, 2009a). Additionally, several studies have used lianas rooted in the vicinity of the tree trunk as a proxy for below-ground competition between lianas and trees (van der Heijden and Phillips, 2009a; Ingwell et al., in press). To assess whether the COI is also an accurate measure of non-crown based liana basal area measurements and therefore can be used in studies focussing in below-ground interactions between lianas and trees, we also measured and counted the lianas within a 1 m radius from the tree trunk. In Tambopata, the detailed liana census was carried out approximately 2 years previous to the COI census. The COI observers were blind with respect to the liana basal area data previously collected. At this site, we also estimated the input time in hours for both the COI survey and the detailed liana survey. For both surveys two observers were used: for the COI, two independent observers, and for the detailed liana survey, one observer and one observer/notetaker.

In Noel Kempff, trees were selected using a stratified design consisting of an approximately equal number of randomly selected trees sampled per 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, and ≥60 cm size-class in each plot. The number of liana stems infesting the tree crown were counted and the diameter of these liana were estimated in 1 cm diameter classes and the mid-point of the diameter class used to calculate liana basal area. However, the basal area of any lianas leaving the tree crown and the basal area of lianas rooted within 1 m of the tree trunk were not estimated.

For subsequent analyses, where necessary, we use the mean COI class rounded to the nearest COI class; results were similar when either the highest or lowest COI class were used (not shown). The detailed liana measurements were grouped in eight different categories to evaluate the accuracy of the COI: (i) liana basal area (liana ba in–liana ba out; Nouragues and Tambopata only), (ii) liana basal area of only those lianas growing into the tree crown (liana ba in), (iii) liana basal area rooted within 1 m (liana ba root; Nouragues and Tambopata only), (iv–vi) these measures controlled for by tree basal area to control tree-size effects (relative liana basal area), (vii) the number of lianas infesting the crown, and (viii) the number of lianas rooted within 1 m from the tree trunk.

2.2. Data analyses

We used data from Nouragues and Tambopata to examine inter-observer bias in each site. The degree of agreement in the assignment of COI by different observers was assessed using the Kendall's coefficient of concordance (Kendall's W), where values close to zero represent no agreement and those close to one indicate complete agreement between the observers. A Spearman's rank test examined whether there is a significant correlation between the ratings of the different observers.

To assess whether the input time for the COI survey was significantly shorter than that of a detailed liana survey, we compared the average input time per tree per plot between the two survey methods using a paired Mann–Whitney U-test.

To assess whether the tree-level detailed liana measures differed amongst the different COI classes, we performed Kruskal–Wallis tests with post hoc Mann–Whitney U-tests with a Hochberg correction (Hochberg, 1988) for each site separately. Tests were also performed for trees in 10–19.9 cm dbh, 20–39.9 cm dbh and ≥40 cm dbh size-classes separately where sample sizes allowed this. On a stand-level, we compared the mean COI and detailed liana measures (all basal area measures were transformed using the natural log) for each of the 19 plots in Nouragues to test whether an increase in mean COI corresponds to an increase in these liana measures by means of a regression model with linear or exponential curve fit, as appropriate.

To examine whether the precision of the COI was high enough to be able to differentiate between the three sites, we used a resampling routine to generate 1000 pseudo-plots for each site with the same size-class distribution, because the sampling protocol and sample size differed slightly between the sites. For each pseudo plot, we randomly selected 50 individuals from each site: 25 of 10–19.9 cm dbh, 15 of 20–39.9 cm dbh, 5 of 40–59.9 cm dbh and 5 of ≥60 cm dbh, and calculated the mean COI and liana basal area (transformed using the natural log) for each pseudo plot. ANOVA and post hoc t-tests with Hochberg correction were performed to investigate if COI and liana basal area differed significantly between the sites.

All statistical analyses were carried out using R 2.9.1 (R Development Core Team, 2009).

3. Results and discussion

In the three sites, on average 37.0 ± 9.1% of the trees did not carry lianas in their crown and 30.0 ± 3.2%, 14.3 ± 3.5%, 10.9 ± 3.3% and 7.8 ± 3.3% of the trees were classified as having 1–25%, 26–50%,

Table 1
(a) Percentage of trees in each of the COI classes and mean (±1 SE) COI and (b) detailed liana measures (mean per tree) for the three Amazonian sites. Relative measures are liana basal area/tree basal area. in = growing in the tree crown, inout = growing in the tree crown–growing out of the tree crown, rooted = rooted within 1 m from tree trunk. In Bolivia, only data on the number and basal area of lianas entering the tree crown were collected NOU, Nouragues, French Guiana; TAM, Tambopata, Peru; PNK, Noel Kempff, Bolivia.

(a)

Site	Location	COI 0 (%)	COI 1 (%)	COI 2 (%)	COI 3 (%)	COI 4 (%)	Mean COI
NOU	French Guiana	31.0	27.5	18.1	13.7	9.8	1.44 ± 0.03
TAM	Peru	32.6	33.7	11.2	11.8	10.7	1.34 ± 0.10
PNK	Bolivia	47.6	28.8	13.5	7.3	2.9	0.89 ± 0.06

(b)

Site	Detailed liana measures (mean per tree)							
	BA in (cm^2)	BA inout (cm^2)	BA rooted (cm^2)	Rel. BA in (cm^2 cm^2)	Rel. BA inout (cm^2 cm^2)	Rel. BA rooted (cm^2 cm^2)	No. lianas in	No. lianas rooted
NOU	31.8 ± 2.4	28.0 ± 2.2	20.9 ± 2.4	0.055 ± 0.003	0.045 ± 0.003	0.050 ± 0.005	3.3 ± 0.1	0.37 ± 0.02
TAM	17.0 ± 2.5	15.3 ± 2.4	12.2 ± 2.5	0.044 ± 0.005	0.037 ± 0.004	0.034 ± 0.006	1.4 ± 0.1	0.56 ± 0.05
PNK	59.2 ± 9.8	NA	NA	0.064 ± 0.007	NA	NA	3.1 ± 0.4	NA

51–75% and >75% of their crown covered by lianas, respectively. The proportion of trees in each COI class and the mean COI and detailed liana measures for each site are indicated in Table 1.

We found a high degree of repeatability in COI classification between observers. Two independent observers classified the liana load of a tree in the same class in 72% and 87% of occasions in Nouragues and Tambopata, respectively. COI classification differed by more than one class for none of the trees in Tambopata and only 2% of trees in Nouragues. When classifications differed, these differences were most often between COI class 1 and 2 (35% in Nouragues and 40% in Tambopata) and class 2 and 3 (28% in Nouragues and 19% in Tambopata). Kendall's W for all comparisons between observers was close to one (Nouragues: $W = 0.87$ [$P < 0.001$, $n = 132$] for all three observers, and 0.91 for both observers 1 and 2 [$P < 0.001$, $n = 880$] and observers 1 and 3 [$P < 0.001$, $n = 1114$] and 0.86 for observers 2 and 3 [$P < 0.001$, $n = 132$]; Tambopata $W = 0.97$, $P < 0.001$, $n = 383$), indicating a high degree of concordance between observers in the classification of COI.

As expected, the input time per tree was much shorter for the COI survey than for the detailed liana survey in Tambopata; on average, the input time for a detailed liana survey was 41.3 h to complete a 1-ha plot, approximately twice as long as for a COI survey (20.3 h; Table 2), significant at the plot level ($n = 3$, $t = 2.80$, $P = 0.05$). This indicates that the COI is an efficient measure of liana loads in the tree crown. Furthermore, TAM-06 had significantly more lianas per tree than the other two plots (data not shown), resulting in a longer input time per tree compared to the other two plots (Table 2). We therefore expect that the differences in input time between the two surveys will increase for sites with more lianas or with a liana infestation which is higher than in Tambopata (52.6%).

Table 2
Comparison of input time between COI survey and detailed liana survey per plot (hours) and per tree (minutes) in Tambopata. Input time for the detailed liana census was based on a 1-ha plot, whilst the input time for the COI survey was based upon a random subset of the trees in the 1-ha plots. The COI input time per plot is estimated by scaling the COI per tree time to the 1-ha plot. Input time includes travel to and from the plots to represent a realistic field situation.

Plot	Per 1-ha plot (h)		Per tree (min)	
	Detailed survey	COI survey	Detailed survey	COI survey
TAM-02	36	23	3.25	2.11
TAM-05	32	18	3.60	2.03
TAM-06	56	20	5.01	1.75
Mean (±1 SD)	41.3 ± 12.9	20.3 ± 2.5	3.95 ± 0.93	1.96 ± 0.19

Generally, the median of most detailed liana measures increased significantly with increasing COI for all three sites (Fig. 1 – only Nouragues shown, see Appendix A supplementary data for Tambopata and Noel Kempff). Total and relative liana basal area of lianas growing into the crown, regardless of whether or not liana basal area was corrected for lianas exiting the crown, and the number of lianas in the crown were all greater for each increasing COI class ($P < 0.001$; K-W $\chi^2 > 227.1$, df = 4, Fig. 1a–d and g). Similar results were obtained when different tree size-classes were considered (Appendix B supplementary data). At the stand-level, the COI was also strongly related to different levels of liana infestation in the crown. Among the 19 Nouragues plots, the stand-level average of total and relative liana basal area growing into the tree crown and the number of lianas per tree crown significantly increased with increasing stand-level COI (all $P < 0.001$), with slightly better fits for the liana basal area values that accounted for lianas exiting the crown (Fig. 2a–d and g).

These results show that the COI can be an accurate measure for number of lianas and liana basal area in the tree crown – whether corrected for lianas exiting the crown or not – both for individual trees and for stands. These results are important for liana research as they (1) indicate that the COI can be used not only as an efficient estimate of the liana pressures experienced by tropical trees, but also as a reliable one, and (2) provide confirmation of the reliability of the several previous studies based on COI surveys (e.g., Clark et al., 1990; Kainer et al., 2006, 2007; Fonseca et al., 2009). However, it remains to be tested whether the COI can be used to detect changes in liana infestation over time.

On the other hand, the COI did not relate well to non-crown based liana measures either on an individual or stand-level. Total and relative basal area of lianas rooted within 1 m of the tree trunk did increase consecutively with COI class, but there was considerable overlap in the liana basal area values associated with each COI class (Fig. 1e and f, Appendix B supplementary data for Tambopata). Furthermore, the number of lianas rooted within 1 metre from the tree trunk only differed between COI class 0 and 3 (Fig. 1h). There was no significant relationship between mean COI and total liana basal area and number of lianas rooted within1 m of the tree trunk on a stand-level (Fig. 2e and h, $P = 0.09$ and $P = 0.16$, respectively). Although relative basal area of lianas rooted in the vicinity of the tree trunk did relate significantly to the stand-level COI (Fig. 2f), the fit of the relationship ($R^2 = 0.23$) was worse than for any of the crown-based liana measures ($R^2 \geq 0.69$). The observation that non-crown based liana measures do not relate to the crown-based COI is perhaps not surprising, as trees may have lianas growing into their crown, but none near to their trunk, and vice versa. For

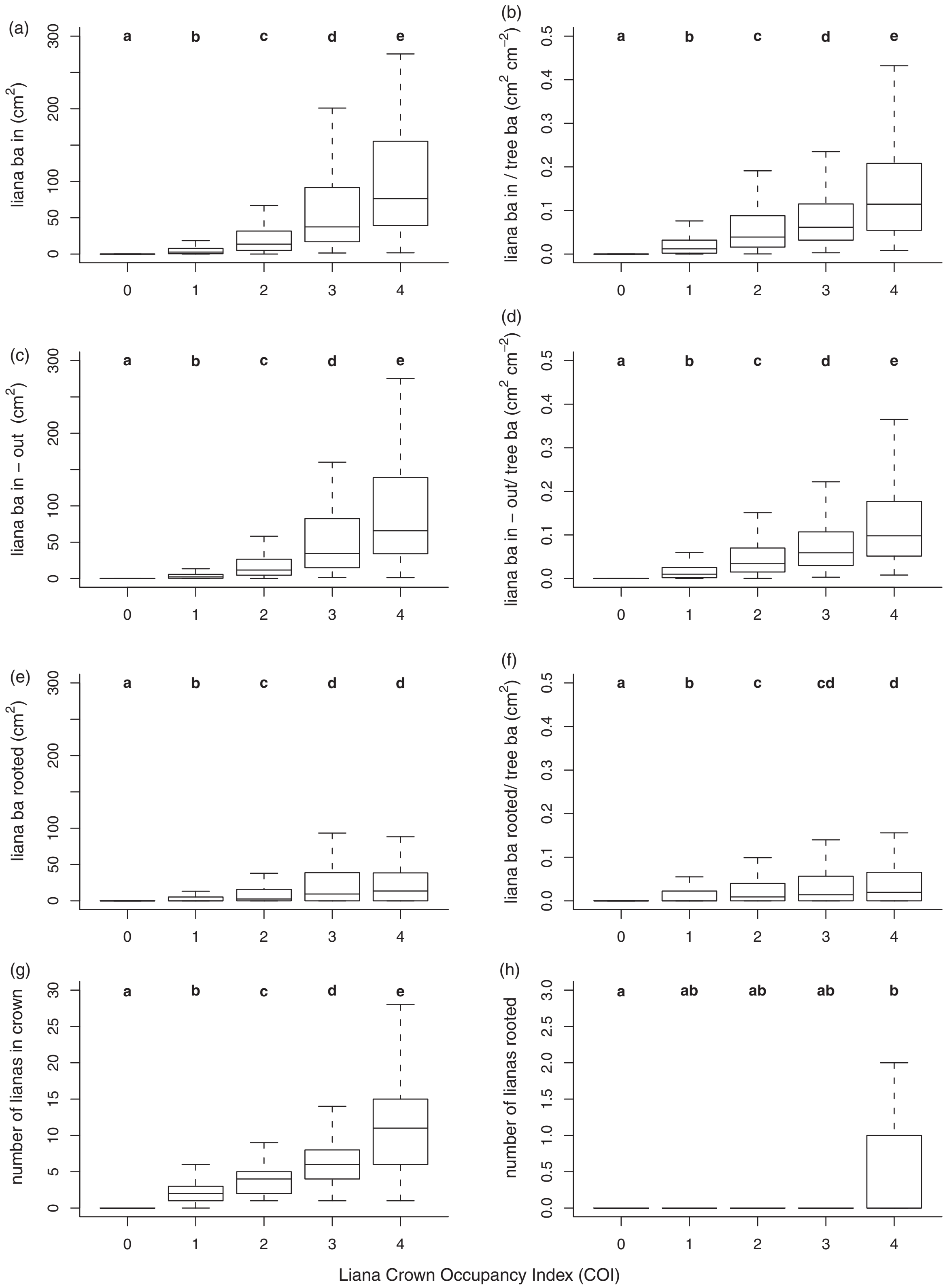

Fig. 1. Boxplots of (a) total and (b) relative liana basal area in the tree crown, (c) total and (d) relative liana basal area in the tree crown corrected for liana basal area exiting the crown, (e) total and (f) relative liana basal area in a 1 m radius from the tree crown, (g) number of lianas in the crown, and (h) number of lianas rooted within 1 m from the tree trunk, for each COI class for Nouragues. Outliers are not shown. Letters above the boxplots (a–e) denote significant differences between COI-categories (Mann–Whitney *U*-test, $P < 0.05$). Results for Tambopata and Noel Kempff are shown in Appendix A supplementary data.

example, in Nouragues, of the trees classified as part of their crown covered by lianas (COI ≥ 1), 28% had no lianas rooted within 1 m from the tree trunk. An extra 5% were classified as having no lianas in their crown, but had lianas rooting in the vicinity of the tree. This suggests that (1) a radius of 1 m of the tree trunk may cover too small of an area to expect a strong relationship with COI, and (2) the COI should not be used as a proxy for below-ground interactions between lianas and trees. Further research is necessary to test

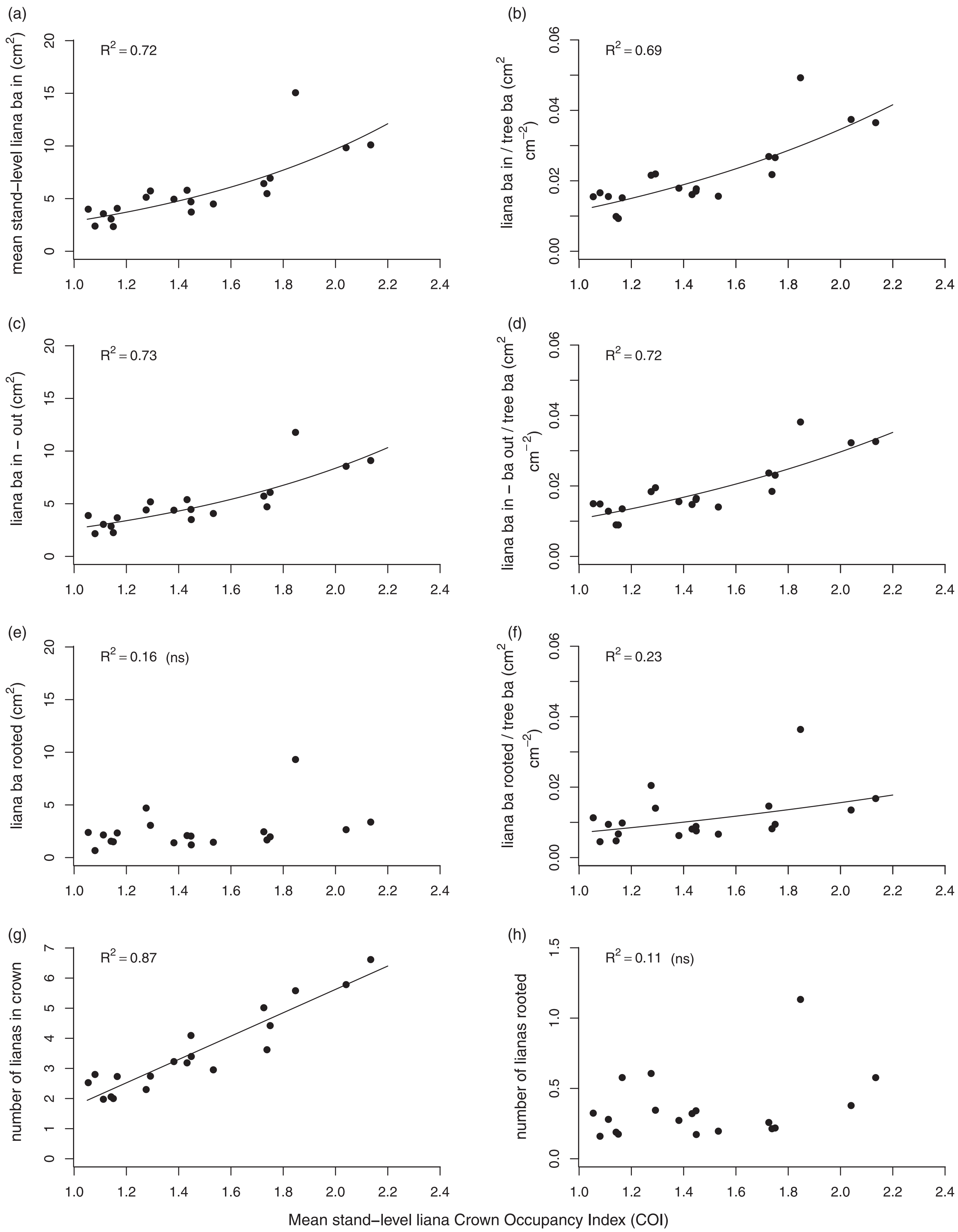

Fig. 2. Relationship between mean stand-level crown occupancy index (COI) and mean stand-level (a) total and (b) relative liana basal area in the tree crown, and (c) total and (d) relative liana basal area in the tree crown corrected for liana basal area exiting the tree crown, (e) total and (f) relative liana basal area rooting within 1 m from the tree trunk, (g) number of lianas in the crown, and (h) number of lianas rooted within 1 m from the tree trunk. Each data point represents one of the 19 plots in Nouragues. Basal area measures were transformed using the natural log, but are back-transformed for graphing purposes. R^2 denotes variance explained by the model, ns indicates an insignificant relationship ($P > 0.05$).

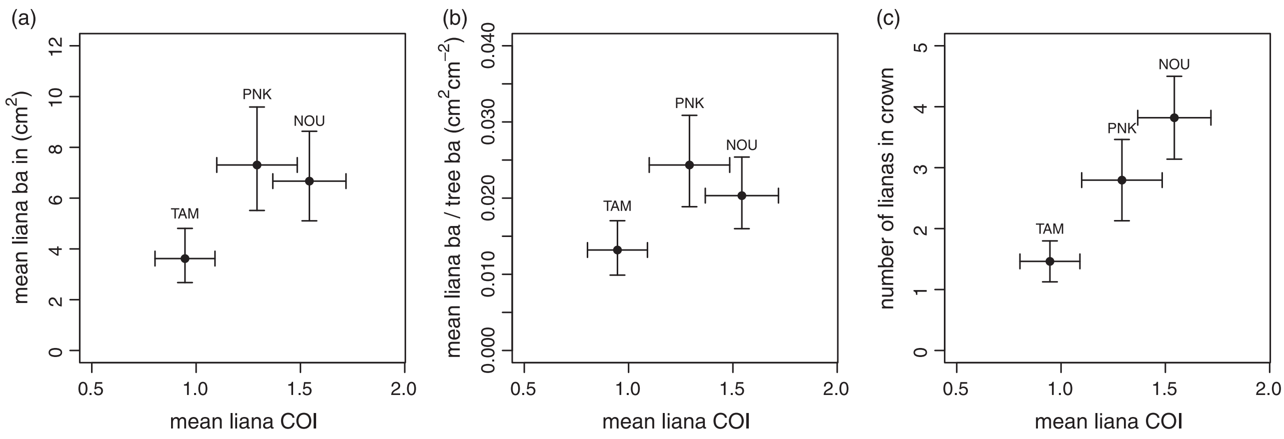

Fig. 3. Mean crown occupancy index (COI) and (a) total, (b) relative liana basal area, and (c) number of lianas in the tree crown for Nouragues (NOU), Noel Kempff (PNK), and Tambopata (TAM) based upon 1000 pseudo-plots (see Section 2). Vertical error bars denote 1 SD of liana measures and the horizontal 1 SD of COI. All sites differ significantly from each other in COI and the detailed liana measures. The analyses were carried out using the natural log of the liana basal area, which were back-transformed for graphing purposes. Due to the use of pseudo-plots and the strong positive skew of the basal area data, results may differ from the average values per site indicated in Table 1.

whether a similar measure with a larger radius will relate better to the COI.

The mean COI differed among the three Amazonian sites ($F = 6058$, $P < 0.001$), with Nouragues having a significantly higher COI and Tambopata a significantly lower COI (Fig. 3). Mean total and relative liana basal area and number of lianas in the crown also differed significantly amongst the sites ($F = 1549$, $P < 0.001$, $F = 834$, $P < 0.001$, $F = 8324$, $P < 0.001$ with df = 1 and $n = 3000$ for total, relative liana basal area and number of lianas, respectively). The mean number of lianas in the crown was clearly increasing with mean COI across sites (Fig. 3c). However, the liana basal area in Noel Kempff was significantly greater than in Nouragues (Fig. 3a and b). Nouragues has a higher liana infestation rate than the two other sites (69.0% of trees, vs. 67.4% for Noel Kempff and 52.6% for Tambopata; Table 1a), which may affect the value of the site-based COI. We therefore also assessed whether total and relative liana basal area differed between the sites when only taking liana-infested trees into account. However, the results were similar to those in which all trees were included (cf. Appendix C supplementary data with Fig. 3). This indicates that trees with a given COI in Nouragues are infested by more, but smaller, lianas, and those in Noel Kempff by fewer, but larger, lianas. The relationship between liana basal area and the COI on an individual tree-level therefore appears to vary somewhat from site-to-site. These site-level differences may be due to different environmental conditions, which affect liana species composition, growth and abundance (Ibarra-Manríquez and Martínez-Ramos, 2002; Schnitzer, 2005; DeWalt et al., 2006; van der Heijden and Phillips, 2008; van der Heijden and Phillips, 2009b). While the COI may therefore be a precise measure when used to discriminate between sites in terms of general liana competition for light, site-level differences in COI do not necessarily correspond to differences in average liana basal area in the tree crown.

4. Conclusions

This is the first attempt to evaluate the overall effectiveness of the liana crown occupancy index (COI). Our findings indicate that the COI varies closely with detailed measures of lianas present in the tree crown both on an individual tree- as well as stand-level basis. This indicates that the COI is an accurate measure to describe liana loads carried by trees and stands. On a site-level, the COI is precise enough to differentiate between sites with different levels of liana canopy competition, but may not be an accurate indicator of site liana basal area in the tree crown. Not surprisingly, the COI is less accurate at indicating the number and basal area of lianas rooting in the proximity of the tree trunk and can therefore not be used as a proxy for below-ground competition between lianas and trees. As the COI is much less time consuming than detailed liana measurements, it may be a preferential method to assess the differences in tree-level, within- and amongst site liana loads.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.05.011.

References

Clark, D.B., Clark, D.A., 1990. Distribution and effects on tree growth of lianas and woody hemi-epiphytes in a Costa Rican tropical wet forest. J. Trop. Ecol. 6, 321–331.
DeWalt, S.J., Ickes, K., Nilus, R., Harms, K.E., Burslem, D.F.R.P., 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. Plant Ecol. 186, 203–216.
Fonseca, M.G., Vidal, E., Maes dos Santos, F.A., 2009. Intraspecific variation in the fruiting of an Amazonian timber tree: implications for management. Biotropica 41, 179–185.
Gerwing, J.J., 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. J. Appl. Ecol. 38, 1264–1276.
Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R.B., Kenfack, D., Martinez-Ramos, M., Parren, M.P.E., Perez-Salicrup, D.R., Putz, F.E., Thomas, D.W., 2006. A standard protocol for liana censuses. Biotropica 38, 256–261.
Grogan, J., Landis, R.M., 2009. Growth history and crown vine coverage are principal factors influencing growth and mortality rates of big-leaf mahogany *Swietenia macrophylla* in Brazil. J. Appl. Ecol. 46, 1283–1291.
Hochberg, Y., 1988. A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75, 800–802.
Honorio Conorado, E.N., Baker, T.R., Phillips, O.L., Pitman, N.C.A., Pennington, R.T., Vásquez Martínez, R., Monteagudo Mendoza, A., Mogollon, H., Davilla Cardoza, N., Rios, M., Garcia-Villacorta, R., Valderrama, E., Ahuite, M., Huamantupa, I., Neill, D.A., Laurance, W.F., Nascimento, H.E.M., Soares de Almeida, S., Killeen, T.J.,

Arroyo, L., Núñez Vargas, P., Freitas Alvarado, L., 2009. Multi-scale comparisons of tree composition in Amazonian terra firme forests. Biogeosciences, 6.

Ibarra-Manríquez, G., Martínez-Ramos, M., 2002. Landscape variation of liana communities in a Neotropical rain forest. Plant Ecol. 160, 91–112.

Ingwell, L.L., Wright, S.J., Becklund, K.K., Hubbell, S.P., Schnitzer, S.A., in press. The impact of lianas on 10-years of tree growth and mortality on Barro Colorado Island, Panama. J. Ecol.

Kainer, K.A., Wadt, L.H.O., Gomes-Sliva, D.A.P., Capanu, M., 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. J. Trop. Ecol. 22, 147–154.

Kainer, K.A., Wadt, L.H.O., Staudhammer, C.L., 2007. Explaining variation in Brazil nut fruit production. Forest Ecol. Manag. 250, 244–255.

Ladwig, L., Meiners, S.J., 2009. Impacts of temperature lianas on tree growth in young deciduous forests. Forest Ecol. Manag. 259, 195–200.

Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T.R., Wright, J., Almeida, S., Arroyo, L., Fredericksen, T.S., Grace, J., Higuchi, N., Killeen, T., Laurence, W.F., Leaño, C., Lewis, S.L., Meir, P., Monteagudo, A., Neill, D., Núñez Vargas, P., Panfill, S.N., Silva, N., Silveira, M., Sombroek, W.G., Valencia, R., Vásquez, R.M., Vieira, I.C.G., Vinceti, B., 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). J. Veg. Sci. 13, 439–450.

O'Brien, J.J., Oberbauer, S.F., Clark, D.B., 2004. Whole tree xylem sap flow response to multiple environmental variables in a wet tropical forest. Plant Cell Environ. 27, 551–567.

Phillips, O.L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T.R., Núñez Vargas, P., 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. Ecology 86, 1250–1258.

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

Putz, F.E., 1991. Silvicultural effects of lianas. In: Putz, F.E., Mooney, H.A. (Eds.), Biology of Vines. Cambridge University Press, Cambridge, UK, pp. 493–501.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, K., Brokaw, N.V.L., Thompson, J., 2004. Liana abundance in a Puerto Rican forest. Forest Ecol. Manag. 190, 33–41.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. Am. Nat. 166, 262–276.

Schnitzer, S.A., Dalling, J.W., Carson, W.P., 2000. The impact of liana on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88, 655–666.

Stevens, G.C., 1987. Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68, 77–81.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prevost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P., Vásquez Martínez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443, 444–447.

van der Heijden, G.M.F., Healey, J.R., Phillips, O.L., 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. J. Veg. Sci. 19, 747–756.

van der Heijden, G.M.F., Phillips, O.L., 2008. What controls liana success in Neotropical forests? Global Ecol. Biogeogr. 17, 372–383.

van der Heijden, G.M.F., Phillips, O.L., 2009a. Liana infestation impacts tree growth in a lowland tropical moist forest. Biogeosciences 6, 2217–2226.

van der Heijden, M.G.A., Phillips, O.L., 2009b. Environmental effects on Neotropical liana species richness. J. Biogeogr. 36, 1561–1572.

Wadt, L.H.O., Kainer, K.A., Gomes-Silva, D.A.P., 2005. Population structure and nut yield of a Bertholletia excelsa stand in Southwestern Amazonia. Forest Ecol. Manag. 211, 371–384.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P., Foster, R.B., 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. J. Trop. Ecol. 21, 307–315.