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Are neotropical predictors of forest epiphyte-host relationships consistent in Indonesia?

Running head: Tropical epiphyte diversity

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Abstract: Epiphytes represent keystone resources for many arthropod and vertebrate species, however their ecology remains poorly explored, especially within the palaeotropics. Several recent studies have examined relationships between epiphyte richness and characteristics of local habitats, although these have all focussed on neotropical forests. Here, we aim to determine whether predictors of neotropical epiphyte richness are consistent at a palaeotropical site. A total of 44 host trees (dbh range 25–288 cm) were sampled at two study sites on Buton Island, Indonesia. For each tree, epiphyte richness and six variables relating to characteristics of the host tree and surrounding habitats were recorded: site (a proxy value for disturbance level and water availability), host above ground biomass (agb), bark texture, exposure, emergence and crown area. Gaussian GLM analyses indicated that the percentage deviance explained in epiphyte richness per host was greatest for agb (20.9%), crown area (19.6%) and site (15.5%); similar to previous findings from the neotropics. Results therefore suggest that high epiphyte diversity within palaeotropical forests is most likely to be found in large tracts of undisturbed forest, supporting large, broad-crowned trees.

Epiphytes are key components of tropical forest ecosystems (Gentry & Dodson 1987), although they remain relatively poorly studied (Barker & Pinard 2001). Methodological advances have facilitated a recent increase in studies of environmental and anthropogenic influences on epiphyte relationships with host trees. Altitude, water availability, bark texture, crown area and heterogeneity, and host size all positively influence epiphyte species richness (Callaway *et al.* 2002, Gentry & Dodson 1987, Woods *et al.* 2015), with negative influences also arising from excess precipitation, and anthropogenic deforestation and degradation (Benzing 1998, Dias-Terceiro *et al.* 2015, Gentry & Dodson 1987). However, these studies have focussed almost exclusively on the neotropics (Nadkarni *et al*. 2011). Epiphyte research elsewhere concentrates more specifically on cataloguing geographic distributions (Hsu & Wolf 2009) or species-specific ecology (Fayle *et al.* 2009, Hsu *et al.* 2012). Therefore, given that each major tropical zone is subject to unique ecological processes and compositions (Corlett & Primack 2011), we cannot yet generalise key factors influencing epiphyte diversity for the broader tropics.

Here, we use canopy surveys to determine whether the principal drivers of epiphyte-host relationships, as identified in the neotropics, are consistent in a palaeotropical forest. We examine the relative influence of multiple environmental variables on vascular epiphyte richness in a lowland Indonesian rain forest. We then construct multivariate models from these data to determine which variables best predict epiphyte richness. In doing so, we aim to test a null hypothesis that epiphytes in a palaeotropical study site will be influenced by the same environmental variables as those identified as significant in the neotropics.

Fieldwork was completed on Pulau Buton, a 5600-km^2 island, located off the south-eastern coast of mainland Sulawesi, Indonesia. Approximately 70% of Buton is covered by seasonal lowland rain forest, with a dry season running June–September, and a wet season running

November–April. Average annual rainfall ranges between 1500 and 2000 mm, and mean average temperatures range between 25°C and 27°C (Whitten *et al*. 2002). A review of the flora of Buton (Powling *et al*. 2015) indicates that over 300 vascular plant species occur on the island, including approximately 150 tree species and more than 50 epiphyte species.

We studied two sites in the South of Buton; one in the interior of the Lambusango Reserve, close to the Lapago forest camp, and the other within the smaller Kakenauwe Reserve, located near the village of Labundo-bundo. These two sites (henceforth 'Lapago' and 'Kakenauwe') were selected as their differences allow for the exploration of environmental variables beyond host morphology. The two sites differ both geologically (Lapago being underlain by a complex mosaic of limestones, sandstones and alluvial material, while Kakenauwe is entirely on karstic limestones), and hydrologically (Lapago, located in a steep-sided valley, allows for greater water retention than the relatively flat Kakenauwe site) (Powling *et al.* 2015). They also differ in levels of disturbance. Kakenauwe, bordering an asphalt road and in close proximity to two villages, has historically been logged and experiences ongoing low-level timber extraction, whereas Lapago experiences little anthropogenic disturbance, due to its isolation (Gillespie *et al.* 2015). Altitude is fairly consistent between sites, ranging between 220 m and 280 m.

Identical sampling techniques were completed at both study sites between June and August 2014, recording data for 44 trees along four transects. Points were systematically marked along transects at 50-m intervals, with the closest climbable tree to each point being sampled.

For each tree, data reporting: (1) above-ground biomass (agb), (2) altitude, (3) crown area (4) height, (5) bark texture, (6) emergence, and (7) epiphyte richness were measured. Variables 1-3 were sampled from the forest floor and the remainder from the canopy.

Agb (kg) was determined by the revised allometric equation for tropical tree agb (Chave *et al*. 2015), using measured diameter at breast height (dbh), defined as 1.3 m or immediately

above buttresses if these were present at 1.3 m, and a specific density value taken from the mean of Indonesian trees (Chave *et al.* 2009, http://datadryad.org/resource/doi:10.5061/dryad.234). Altitude (m asl) was recorded by GPS, and crown area was estimated by multiplying together the crown extents along North-South and East-West axes.

To measure the remaining variables, single-rope techniques were used to ascend to the highest safe point within the crown. A weighted tape measure was then lowered to record observer height and an estimate of remaining distance to the top of the tree was added to provide a metric of tree height. Bark texture was characterised using a three-point index of flakiness, roughness and fissuredness. Indices were ranked: 1 – characteristic not present; 2 – characteristic present; or 3 – characteristic strongly present (Male & Roberts 2005). Emergence (yes/no) was determined by whether the tree was >5 m taller than surrounding trees. Epiphyte richness was counted by scanning foliage above the observers' height, and then slowly descending the tree while searching for epiphytes on all sides of the tree. Epiphytes were identified to a morphospecies level (Cardelus *et al.* 2006), in response to local restrictions on sampling within protected areas.

Following data collection, we examined the relative importance of different environmental variables through multivariate analyses, incorporating the seven variables measured at each tree, plus site (Lapago or Kakenauwe). Data exploration was performed and severely skewed variables transformed to achieve Gaussian distributions (epiphyte richness, host agb, bark fissuredness and crown area were transformed by log10 and Bark flakiness by log10 twice).

Predictor variables with the highest Variance Inflation Factors (VIFs) were sequentially removed to create three models where no VIF exceeded 2, minimising intercorrelation (Zuur *et al.* 2010). Models 1 and 2 prioritised retention of different, non-collinear, host-size predictor variables (host agb and crown area), while model 3 focussed solely on bark texture.

Bidirectional elimination by stepwise regression further reduced these models to form Minimum Adequate Models (MAMs), which were found, by analysis of deviance, to have no significant difference from the full models. Gaussian Generalised Linear Models (GLMs) were run for each MAM, calculating the percentage deviance of epiphyte species richness they were able to explain. Where MAMs retained more than one predictor variable, GLMs were also run removing one variable at a time to calculate their relative influence on the deviance of the response variable. P-values from each GLM were used in false discovery rate end-point adjustment to create a new alpha value of 0.029 by which the significance of each variable was determined. All analyses were carried out in R version 3.2.1.

From our sample of 44 trees (18 in Lapago and 26 in Kakenauwe), a total of 275 individual epiphytes from 74 taxa (60 in Lapago and 41 in Kakenauwe) were recorded. Trees sampled in Lapago hosted a significantly higher number of epiphyte species (8.94 ± 2.42) compared to those in Kakenauwe (4.12 ± 1.17) (Mann-Whitney U = 73.5, P < 0.001)). GLMs (Table 1; Figure 1) show that epiphyte richness was mainly influenced by tree size (as indicated by crown area and host agb), and variables associated with the attributes of the two study sites.

Our findings support the hypothesis that the principal drivers of epiphyte epiphyte-host relationships identified in the neotropics (i.e. host size, crown area and disturbance level) remain consistent in our palaeotropical study site on Buton Island. The significance of most of these findings is expected, e.g. host size and crown area are known to relate to available substrate accumulation and surface area of branches and trunk for phorophyte colonisation (Flores-Placios & García-Franco 2006, Goodman *et al.* 2014), and disturbance level is known to influence host size, resulting in declining epiphyte populations (Es'kov 2013). Interestingly, bark texture, previously indicated as being a driver of epiphyte diversity in the

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neotropics (Callaway *et al.* 2002, Gentry & Dodson 1987), was found not to be significant in this study, although this could be due to the categorical nature of the bark data collected. Bark fissuredness was, however, selected to be used in minimum adequate models (Table 1) due to its strength of correlation with species richness, suggesting some cross-validation of the neotropical conclusions. Another variable shown to be an important driver of epiphyte diversity in the neotropics is water availability (Callaway *et al.* 2002, Laube & Zotz 2003). We could not test this directly in this study due to the lack of local year-round meteorological data. However, it is likely that Lapago, which possesses more alluvial sediment and a central river within its steep sided valley, has better water availability than the fast-draining limestones of Kakenauwe (Powling *et al.* 2015). Thus the significance of the site variable may be partially explained by differences in water resources.

In conclusion, this study demonstrates, by assessing a wide range of variables for the first time in palaeotropical literature, that epiphyte richness on Buton is most strongly influenced by the same key drivers as those described in the neotropics. While some variables require further investigation, our findings suggest that the best means of maintaining high epiphyte diversity in the palaeotropics is by protecting primary forests which support high densities of large, broad-crowned trees; a conservation recommendation echoed for other taxa (Barlow *et al.* 2007) although not specifically for epiphytes of the palaeotropics before. While further research is required to develop a full understanding of regional influences on epiphyte diversity, this recommendation provides important insight for forest managers to account for enigmatic and often overlooked canopy species.

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Tables

Table 1. Gaussian Generalised Linear Models, simplified into minimum adequate models using elimination by stepwise regression, to explain deviance in epiphyte species richness$_{log10}$ on host trees on Buton Island, Indonesia. Akaike Information Criterion (AIC) shows the parsimony of each model. Asterisks (*) denote significant P-values (α FDR = 0.029).

	Minimum adequate model	P-value (FDR = 0.029)	AIC	% Deviance explained
Model 1 Altitude, Bark flakiness$_{log10log10}$, Bark roughness, Bark fissuredness$_{log10}$, Canopy openness, Emergence, Exposure, Host agb$_{log10}$, Site	- Host agb$_{log10}$ Site	- <0.001* <0.001*	-17.89	51.3 20.9 15.5
Model 2 Altitude, Bark Flakiness$_{log10log10}$, Bark Roughness, Bark Fissuredness$_{log10}$, Canopy Openness, Crown Area$_{log10}$, Emergence, Exposure, Site	- Bark Fissuredness$_{log10}$ Crown Area$_{log10}$ Exposure Site	- 0.092 <0.001* 0.157 0.017*	-15.07	52.6 3.62 19.6 2.53 7.51
Model 3 Bark Flakiness$_{log10log10}$, Bark Roughness, Bark Fissuredness$_{log10}$	- Bark Fissuredness$_{log10}$	- 0.063	- 8.10	- 8.00

Legends to Figures

Figure 1. Epiphyte species richness$_{log10}$ versus host crown area$_{log10}$ (m^2) (a) and host agb$_{log10}$ (kg) (b) on Buton Island, Indonesia. GLM regression lines shown on both graphs.
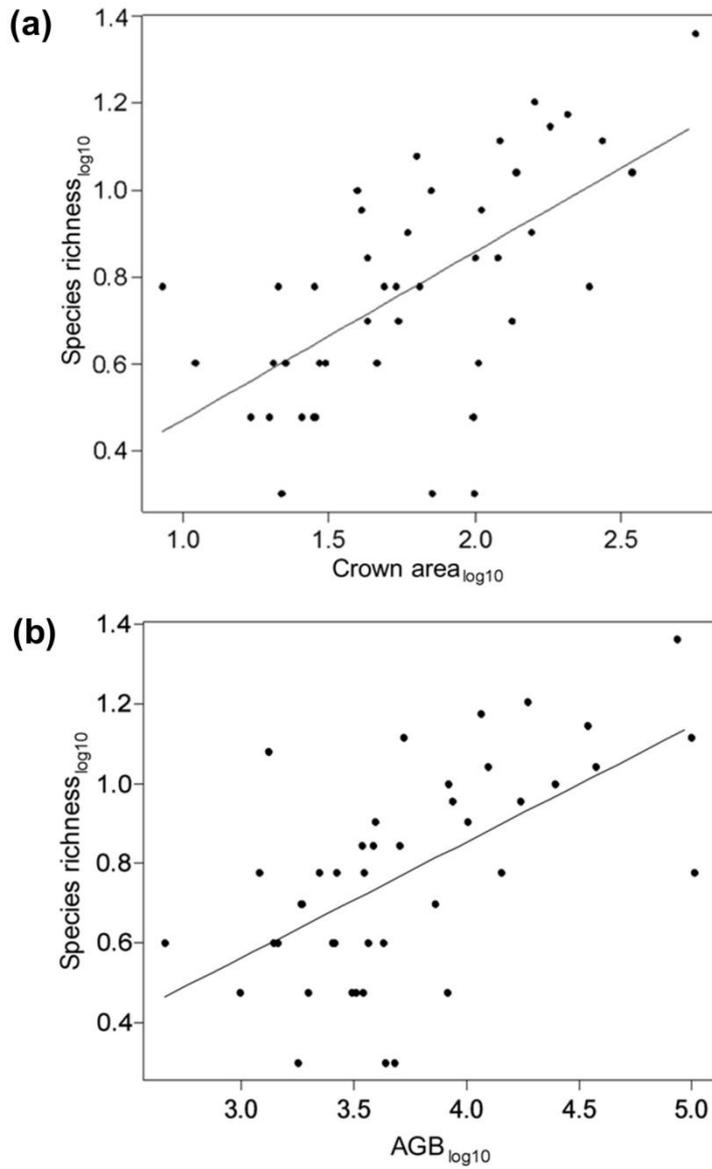

Figure 1.