

## The Effect of Rain Forest Canopy Architecture on the Distribution of Epiphytic Ferns (*Asplenium* spp.) in Sabah, Malaysia

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### ABSTRACT

Epiphytic plants are a dominant component of the rain forest canopy biota. They represent a significant proportion of canopy plant biomass and diversity, play a key role in nutrient cycling, and support highly abundant and diverse animal communities. Understanding the factors affecting their distribution in this three-dimensional habitat is consequently of great importance, not least because they may be particularly vulnerable to climate change and habitat conversion. Here we investigate how canopy architecture affects the distribution of two species of bird's nest fern (*Asplenium* spp.) in pristine rain forest. Both species were found at high abundances (*Asplenium phyllitidis*: 136/ha, SE  $\pm$  31.6, *Asplenium nidus*: 44/ha, SE  $\pm$  9.2) and their distributions were differentially affected by canopy architecture. *Asplenium phyllitidis* was found only at heights < 30 m in areas with a thicker lower canopy layer. *Asplenium nidus* was found at all heights in the canopy and was associated with emergent trees and areas with an open understory. Larger *A. phyllitidis* were found higher in the canopy while larger *A. nidus* were found on trunks and branches with a wider diameter. *Asplenium nidus* seems adapted to withstand the hot dry conditions in the upper canopy and in gaps, and its size is consequently limited only by the size of its support. *Asplenium phyllitidis* is dominant in areas that are cooler and damper, and so the growth rate of individuals may be limited by light levels. We discuss possible implications of this partitioning for epiphyte communities in the face of climate change and habitat conversion.

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*Key words:* *Asplenium nidus*, *Asplenium phyllitidis*; bird's nest fern; climate change; habitat conversion; microclimate; vertical stratification.

EPIPHYTIC PLANTS ARE A MAJOR CONTRIBUTOR to vascular plant diversity (Hsu *et al.* 2002) and biomass (Tanner 1980, Nadkarni 1984) in the canopies of many tropical forests. They contain a high proportion of the canopy nutrient capital (Nadkarni 1984) and can support diverse communities of animals (Ellwood *et al.* 2002, Ellwood & Foster 2004). They are also ideal for use as microcosms for investigating questions in community ecology (*e.g.*, Richardson 1999). Understanding how epiphyte species partition the heterogeneous canopy environment is therefore of great importance.

One of the most abundant epiphytic plants in the old-world tropics is the bird's nest fern (*Asplenium* spp.; Fig. S1). Their range extends from the east coast of Africa through India and SE Asia to Japan, northern Australia and many islands in the western Pacific (Holtum 1976), and they are found both in primary forest and in human-modified habitats, such as logged forest and oil palm plantations (Turner 2005).

Bird's nest ferns play an important role in the ecology of old-world tropical forest canopies. They are litter-basket epiphytes, intercepting falling leaf litter and using the nutrients resulting from the decomposition of these leaves. One consequence of this is an increase in nutrient content of stemflow water passing through the ferns (Turner *et al.* 2007), which may have an effect on the plant and animal communities living below them. They also intercept

and store water in their sponge-like root mass and consequently buffer local microclimate in the canopy (Turner & Foster 2006). As a result they provide an important refuge for animals ranging from arthropods to bats, away from the hot dry conditions found elsewhere in the canopy (Hodgkison *et al.* 2003, Ellwood & Foster 2004). They are often found growing in mats with many other species of epiphyte (T. M. Fayle, pers. obs.), presumably because their nutrient-rich cores provide an ideal site for germination. Therefore these ferns are of great importance in the ecology of other canopy plants and animals, and deducing which factors affect their distribution is an important step toward understanding the workings of the rain forest ecosystem.

Microclimate may be of particular importance in determining the distribution of bird's nest ferns. In the canopy temperature and humidity vary a great deal, mainly as a consequence of differences in canopy architecture (Dial *et al.* 2006). Despite the fact that bird's nest ferns can absorb and store water they are still susceptible to drought (Freiberg & Turton 2007). The microclimate in an area will therefore affect the probability of fern mortality and consequently will affect the distribution of different species. This is of particular concern because the close ecological ties between epiphytes and microclimate may make them susceptible to climate change (Mondragon *et al.* 2004) and habitat conversion (Padmawathe *et al.* 2004). Mean global temperature is predicted to increase by 1.8–4°C by 2090–2099 compared with 1980–1999 (IPCC 2007) and this will presumably cause higher rates of

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epiphyte mortality through desiccation. In addition, extreme climatic conditions, such as the SE Asian droughts associated with the El Niño Southern Oscillation (*e.g.*, Harrison 2001) have increased in frequency in recent years (Guilderson & Schrag 1998). Habitat conversion by humans, such as logging and conversion to plantations, will affect the canopy architecture and consequently the microclimate (Turner & Foster 2006) and would therefore also be expected to result in changes in the epiphytic community (Padmawathe *et al.* 2004).

This study examines how canopy architecture influences the distributions of different species of bird's nest ferns in pristine rain forest.

## METHODS

**STUDY SITE.**—Surveys for ferns were carried out in primary forest near Danum Valley Field Centre in Danum Valley Conservation Area, Sabah, Malaysia (5°01' N, 117°49' E) from April to July 2006. Average annual temperature in the area is 26.7°C and average annual rainfall 2669 mm, with no strong seasonality (Walsh & Newbery 1999). The area is mainly lowland evergreen dipterocarp forest on orthic Acrisol soil, developed on sandstone and mudstone (Marsh & Greer 1992).

**SAMPLE DESIGN AND FIELD MEASURES.**—To understand which aspects of canopy architecture are important for determining abundances of these epiphytes, surveys for ferns were carried out over twenty 20 × 100 m transects. These were randomly positioned in the main trail grid area within 2 km of the field center. All bird's nest ferns within these transects were surveyed using a laser rangefinder (Impulse 200 LR, Laser Technology Incorporated, Englewood, Colorado, U.S.A.) and compass to give three-dimensional coordinates and each was putatively identified to species with binoculars using keys in Holttum (1976). Immature ferns do not have sori (bodies containing spores) and consequently it was not possible to identify them in the field. Three canopy architecture variables that we hypothesized would be important in determining fern distribution were recorded for each transect. Understorey density was measured at head height by taking the average horizontal distance to any sort of vegetation using a laser rangefinder and was assessed at 12 evenly spaced bearings. Lower canopy layer thickness (the vertical height above ground of the continuous canopy layer) was measured using a laser rangefinder. The number of trees per transect with at least some bare trunk above the lower canopy (emergents) was counted. Altitude was measured from contour maps of the area and the gradient of the relief was measured using a laser rangefinder. All of these variables were measured at 10 evenly spaced points along each transect.

A subset of ferns was selected to sample for the purpose of determining local habitat variables affecting fern species and size, and to use molecular techniques to confirm identification. This was necessary as bird's nest ferns have relatively few morphological characters on which to base identification (Murakami *et al.* 2000), particularly when no sori are present. Ferns were sampled in a stratified random manner with respect to size to assess which canopy architecture variables affect fern growth rate and size-dependent

mortality. Frond samples were taken from each fern and placed in Ziploc bags containing silica gel. Ferns were collected into plastic bags, dried to constant weight, and their final weights recorded. Ferns were collected using a combination of ground-based, ladder-based, and rope access (single rope technique) methods. At the site of each fern the diameter of the substrate plant was measured, canopy cover assessed using a standard concave spherical densiometer (Lemmon 1956), and leaf density calculated using a laser rangefinder following the method of Dial *et al.* (2006). This method allows the calculation of the leaf density in an area from measurements of the distance to leaf surfaces from a point.

**MOLECULAR IDENTIFICATION OF FERNS.**—To make positive species-level identification of collected ferns we produced DNA sequences from field samples and compared them to established reference sequences. An initial search of the literature was carried out to identify an appropriate chloroplast region to use to discriminate between fern samples. The *trnL* intron has been used in a number of studies to discriminate between *Asplenium* species and this has produced a large number of reference sequences to compare our samples against (Trewick *et al.* 2002, Van den heede *et al.* 2003, Schneider *et al.* 2005). DNA was extracted from a 1.5 × 1.5 cm piece of fern leaf using a PowerPlant DNA isolation Kit (Mo Bio, Carlsbad, California, U.S.A.) according to the manufacturer's instructions. The plastid *trnL* intron (*ca* 350 bp) was amplified from fern DNA using *Taq* DNA polymerase with the universal chloroplast primers E and F from Taberlet *et al.* (1991). PCR reactions were carried out in the presence of 0.2 mM dNTPs, 20 pmol of each primer, and the manufacturer's reaction buffer in 50 µL reactions (PCR conditions: 95°C for 2 min; 10 cycles at 95°C for 1 min, 52°C for 1 min and 72°C for 2 min; 19 cycles at 95°C for 30 sec, 52°C for 1 min and 72°C for 3 min; and 1 cycle at 95°C for 30 sec, 52°C for 1 min and 72°C for 10 min on a Gradient 96 Robocycler [Stratagene, La Jolla, California, U.S.A.]). PCR products were purified using Qiagen's (Crawley, UK) QIAquick PCR Purification Kit following the manufacturer's instructions and sequencing was conducted under BigDye™ terminator cycling conditions and run using Automatic Sequencer 3730xl. DNA sequences were checked by eye and compared against reference sequences (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>) using the Blast algorithm (Altschul *et al.* 1990). This analysis identified two separate species (*Asplenium nidus* L. and *Asplenium phyllitidis* D. Don) from our field samples. We assigned uncollected unidentified ferns to species on the basis of these proportions for the purposes of calculating densities of the different species. However, the unidentified ferns were treated separately during statistical analysis.

**STATISTICAL ANALYSIS.**—The effects of canopy architecture and other environmental variables on fern abundances and weights were assessed using general linear models. All fern counts were square root transformed and average distance to vegetation was  $\log_{10}(x)$  transformed so that model residuals were normally distributed. The effects of canopy architecture on fern dry weight were assessed separately for each species of fern. Immature ferns were excluded from this analysis as they did not exhibit a large range of sizes. An outlying canopy cover data point was completely responsible for an effect of canopy cover on the weight of

*A. phyllitidis*; thus results presented here are for analysis without that data point. All variables were included in initial models and then the least significant variables progressively removed until all remaining variables had  $P$  values of  $< 0.1$ . Differences in the vertical stratification of the two fern species were analyzed using a chi-square test carried out on counts within 10 m height classes. Counts for ferns  $> 30$  m were lumped for each species. Unidentified ferns were excluded from this analysis. For the ferns that were collected, a logistic regression was used to assess how local canopy architecture determined which species would be present at a particular location. Height and substrate diameter were  $\log_{10}(x)$  transformed, while canopy cover was arcsine-square root transformed to linearize relationships between independent variables (Maindonald & Braun 2007).

## RESULTS

In total, 719 ferns at heights from ground level to 54 m were surveyed over the 20 transects. Both species of bird's nest ferns recorded in the rain forest in Danum Valley were highly abundant with *A. phyllitidis* occurring at a mean abundance of 136/ha ( $\pm 31.6$  SE) and *A. nidus* at 44/ha ( $\pm 9.2$ ). Densities of ferns were highly variable across transects with a range of 0–414/ha for *A. phyllitidis* and 0–146/ha for *A. nidus*. Molecular identification confirmed the field identifications in 93 percent of cases where a

species name had been assigned in the field and there was no bias in terms of the direction of misidentification (two *A. phyllitidis* were misidentified as *A. nidus* and two vice versa). Of the 19 immature ferns that could not be identified in the field, 11 were *A. phyllitidis* and eight were *A. nidus*.

*Asplenium phyllitidis* occurred at higher densities in areas of forest with thicker lower canopy layers (GLM, lower canopy layer thickness:  $F_{1,18} = 15.7$ ,  $P = 0.001$ ; Fig. 1A). *Asplenium nidus* was found at higher densities in areas of forest with greater numbers of emergent trees and more open understories (number of emergents:  $F_{1,17} = 19.6$ ,  $P < 0.001$ ; Fig. 1B; understory density:  $F_{1,17} = 7.15$ ,  $P = 0.016$ ). Immature ferns were more abundant at higher altitudes and in areas of forest with thicker lower canopy layers (altitude:  $F_{1,17} = 7.99$ ,  $P = 0.012$ ; lower canopy layer thickness:  $F_{1,17} = 11.4$ ,  $P = 0.004$ ). Larger *A. phyllitidis* were found higher in the canopy (canopy height:  $F_{1,54} = 14.1$ ,  $P < 0.001$ ; Fig. 1C), while larger *A. nidus* were found on wider branches and trunks (substrate diameter:  $F_{1,18} = 56.2$ ,  $P < 0.001$ ; Fig. 1D).

The ferns were also stratified with respect to height in the canopy (*A. phyllitidis* vs. *A. nidus*,  $\chi^2 = 152$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 2). *Asplenium nidus* was found at all heights up to 60 m, while *A. phyllitidis* and immature ferns were found only up to 30 m. For ferns where local canopy architecture variables were assessed, *A. nidus* was found higher than *A. phyllitidis*, although this effect

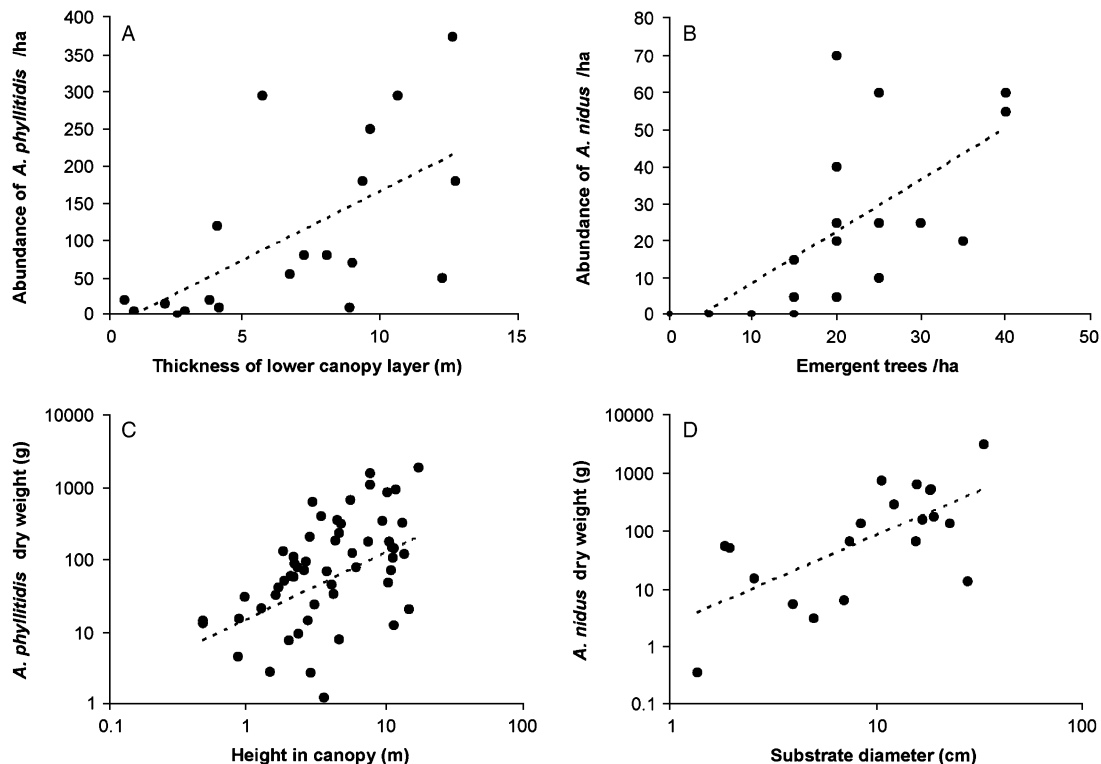


FIGURE 1. The relationship between the abundances and sizes of the two species of *Asplenium* and different aspects of rain forest canopy architecture. (A) Higher densities of *A. phyllitidis* were found in areas with a thicker lower canopy layer ( $N = 20$ ). (B) Higher densities of *A. nidus* were found in areas with larger numbers of emergent trees and more open understories (only the relationship with emergent trees is shown here,  $N = 20$ ). (C) Larger *A. phyllitidis* were found higher in the canopy ( $N = 59$ ). (D) Larger *A. nidus* were found on wider branches and trunks ( $N = 20$ ). Note the logarithmic scale on both axes for plots C and D.

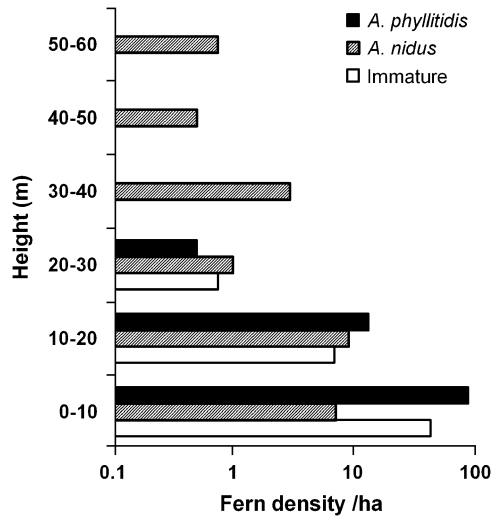


FIGURE 2. Vertical stratification of the two species of fern in the canopy. Only *Asplenium nidus* was found at heights > 30 m, while both *A. nidus* and *A. phyllitidis* were found at heights < 30 m. Immature ferns were also only found at heights < 30 m. Note the logarithmic scale on the x-axis.

was marginally non-significant (logistic regression, height:  $Z = -1.89$ ,  $P = 0.059$ , odds ratio = 0.24). No other variables had a significant effect on the identities of this subset of ferns.

## DISCUSSION

Despite coexisting in the same forest, the two species of bird's nest ferns were found to have different habitat requirements (Fig. S2). *Asplenium phyllitidis* was found only beneath the continuous canopy layer, thus limiting it to heights < 30 m. Within this layer, larger *A. phyllitidis* individuals were found higher in the canopy. *Asplenium nidus* was found at all heights in the canopy, in particular in association with emergent trees and in areas with an open understory. The diameter of the supporting structure was the only factor to limit the size of *A. nidus* individuals. Local canopy architecture did not have an effect on the species of fern collected at a site, beyond the effect of height. Hence, canopy architecture at the scale of a transect (0.2 ha) is important in determining the abundance of the two species, but canopy architecture at the local scale is important in determining how large individuals of these species can grow.

This difference in response to canopy architecture indicates that the populations of the two species have different factors limiting their abundances. There are two potential limiting factors for populations of epiphytes: dispersal limitation (Martin *et al.* 2008) and mortality (Lopez-Villalobos *et al.* 2008). The nature of responses of the two species indicates that both of these factors are important. There are thought to be two main sources of epiphyte mortality: dislodgement and drought (Lopez-Villalobos *et al.* 2008). While it is possible that the two species experience different rates of dislodgement, it seems that drought is the main source of mortality for bird's nest ferns. *Asplenium nidus* is better at withstanding hot dry conditions, whereas *A. phyllitidis* thrives in the

cooler, damper understory. But the effect of these canopy architecture variables on fern abundance is seen not at the local level, but at the transect level. It may be that large-scale canopy architecture has a greater impact on local microclimate than local scale canopy architecture. In addition, large-scale differences in architecture will affect the abundances of the two species over a large area, consequently altering the propagule pressure on any one potential colonization site within that area. Hence, both dispersal limitation and mortality are responsible for the observed differences in distribution between the two species.

While not being important in determining fern distribution, local-scale architecture does have an impact on fern size. *Asplenium phyllitidis*, being only able to inhabit relatively cool, damp, and presumably dark microhabitats, may be affected by light availability. Higher in the canopy, where it is brighter, it is able to grow to larger sizes. *Asplenium nidus* grows in more exposed areas and is consequently not light limited. Only the size of its substrate trunk or branch limits its growth rate. This suggests that dislodgement may have an impact on the size distribution of *A. nidus*. Large ferns on small trunks and branches are more likely to be dislodged causing a correlation between substrate diameter and fern size. Surprisingly, there was no relationship between canopy openness, as assessed by the spherical densiometer, and any aspect of fern distribution. This may be because densiometer readings do not tend to correlate well with light conditions (Engelbrecht & Herz 2001). Instead they measure canopy openness for only an area directly above the point of measurement, which may not always correlate with conditions experienced by individual ferns.

These distributional relationships with canopy architecture will have effects on the many animals and plants that live in association with bird's nest ferns. In areas with thicker lower canopy layers, more emergent trees, and more open understories, there will be larger numbers of ferns and consequently higher densities of the animals and plants supported by them. Larger ferns support a greater biomass of arthropods (Ellwood & Foster 2004) and presumably the same is true for associated plant communities. This means that areas with higher canopies and wider supporting structures will have more associated animals and plants as they support larger ferns. In addition, we would expect the larger ferns found in these areas to enrich stemflow water (Turner *et al.* 2007) to a greater degree. The vertical stratification of ferns found in this study mirrors the pattern seen in arthropod abundance (Dial *et al.* 2006), with a peak in numbers of ferns and arthropods at heights < 30 m. While it may be that both groups are responding in the same way to canopy architecture, at least some of this effect may be due to the higher abundance of ferns supporting more arthropods, especially given the high densities of ferns in pristine rain forest (up to 560/ha).

Given the keystone role that bird's nest ferns play in pristine rain forest it is useful to speculate on how current ecological challenges will affect them. The information presented here on the two fern species' ecology allows us to make qualitative predictions of the impacts of climate change and habitat conversion on them. In a way that parallels the predicted shifts of species ranges up altitudinal gradients we would expect the canopy fauna to move down as a greater proportion of the canopy becomes hot and dry. If

temperatures increase then we would expect the distribution of *A. nidus* to become more biased toward the lower canopy, with possible increases in overall abundance, while *A. phyllitidis* would decrease in overall abundance as its favored cool damp understory microclimate disappears. A similar effect might occur if an area of rain forest is logged or converted to plantation. This can lead to species usually characteristic of the high canopy inhabiting lower canopy layers as the height and complexity of the forest is reduced (Sutton 2008). Again we would expect *A. nidus* to increase in abundance and to have a lower distribution in the canopy, while *A. phyllitidis* would decrease in abundance. Habitat conversion is one of the greatest threats to biodiversity globally, and in Malaysia in particular (Turner *et al.* 2008) where logging of primary forest has been extensive, and conversion of forest to oil palm plantation is widespread. Bird's nest ferns are abundant in these modified habitats with densities up to 15 m in the canopy of 53 ferns/ha in logged forest and 117 ferns/ha in oil palm plantations (Turner 2005). Despite this, in oil palm plantations all bird's nest ferns appear to belong to a single species: *A. nidus* (Piggott 1988, Nadarajah & Nawawi 1993). Oil palm plantations have a hot dry microclimate (Turner & Foster 2006) similar to that found in the high canopy and have consequently been colonized by the species usually found in that stratum of pristine forest.

In this study we have demonstrated that epiphytes partition the complex environment of the canopy with respect to its architecture. Species respond in different ways to changes in small- and large-scale canopy architecture and these responses will affect the many other plants and animals that live in association with the ferns. Such differential responses may leave some species more vulnerable to climate change and habitat conversion than others.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Bird's nest ferns (*Asplenium* spp) in the high canopy of rain forest in Danum Valley.

FIGURE S2. Schematic diagram of the distribution of the two species of ferns in relation to canopy architecture.

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## LITERATURE CITED

- ALTSCHUL, S. F., W. GISH, W. MILLER, E. W. MYERS, AND D. J. LIPMAN. 1990. Basic local alignment search tool. *J. Mol. Biol.* 215: 403–410.
- DIAL, R., M. D. F. ELLWOOD, E. C. TURNER, AND W. A. FOSTER. 2006. Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. *Biotropica* 38: 643–652.
- ELLWOOD, M. D. F., AND W. A. FOSTER. 2004. Doubling the estimate of invertebrate biomass in a rain forest canopy. *Nature* 429: 549–551.
- ELLWOOD, M. D. F., D. T. JONES, AND W. A. FOSTER. 2002. Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites and other invertebrates. *Biotropica* 34: 575–583.
- ENGELBRECHT, B. M. J., AND H. M. HERZ. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. *J. Trop. Ecol.* 17: 207–224.
- FREIBERG, M., AND S. M. TURTON. 2007. Importance of drought on the distribution of the birds nest fern, *Asplenium nidus*, in the canopy of a lowland tropical rain forest in north-eastern Australia. *Aust. Ecol.* 32: 70–76.
- GUILDERSON, T. P., AND D. P. SCHRAG. 1998. Abrupt shift in subsurface temperatures in the tropical Pacific associated with changes in El Niño. *Science* 281: 240–243.
- HARRISON, R. D. 2001. Drought and the consequences of El Niño in Borneo: A case study of figs. *Popul. Ecol.* 43: 63–75.
- HODGKINSON, R., S. T. BALDING, Z. AKBAR, AND T. H. KUNZ. 2003. Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *J. Trop. Ecol.* 19: 667–676.
- HOLTUM, R. E. 1976. *Asplenium* Linn., sect. *Thamnopteris* Presl. *Gard. Bull. Singapore* 27: 143–154.
- HSU, C.-C., F.-W. HORNG, AND C.-M. KUO. 2002. Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan. *J. Trop. Ecol.* 18: 659–670.
- IPCC. 2007. Climate change 2007: Synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- LEMMON, P. E. 1956. A spherical densiometer for estimating forest overstorey density. *For. Sci.* 2: 314–320.
- LOPEZ-VILLALOBOS, A., A. FLORES-PALACIOS, AND R. ORTIZ-PULIDO. 2008. The relationship between bark peeling rate and the distribution and mortality of two epiphyte species. *Plant Ecol.* 198: 265–274.
- MAINDONALD, J., AND J. BRAUN. 2007. Data analysis and graphics using R. Cambridge University Press, Cambridge, UK.
- MARIN, A. C., J. H. D. WOLF, J. G. B. OOSTERMEIJER, AND J. C. M. D. NIJS. 2008. Establishment of epiphytic bromeliads in successional tropical premontane forests in costa rica. *Biotropica* 40: 441–448.
- MARSH, C. W., AND A. G. GREER. 1992. Forest land-use in Sabah, Malaysia: And introduction to Danum Valley. *Philos. Trans. R. Soc. London, Ser. B* 335: 331–339.
- MONDRAGON, D., R. DURAN, I. RAMIREZ, AND T. VALVERDE. 2004. Temporal variation in the demography of the clonal epiphyte *Tillandsia brachycaulos* (Bromeliaceae) in the Yucatan Peninsula, Mexico. *J. Trop. Ecol.* 20: 189–200.
- MURAKAMI, N., Y. YATABE, H. IWASAKA, D. DARNAEDI, AND K. IWATSUKI. 2000. Molecular  $\alpha$ -taxonomy of a morphologically simple fern *Asplenium nidus* complex from Mt. Halumin National Park, Indonesia. In M. Kato (Ed.). *The biology of biodiversity*. pp. 53–66. Springer-Verlag, Tokyo, Japan.

- NADARAJAH, P., AND A. NAWAWI. 1993. Mycorrhizal status of epiphytes in oil palm plantations. *Mycorrhiza* 4: 21–25.
- NADKARNI, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical Elfin forest. *Biotropica* 16: 249–256.
- PADMAWATHE, R., Q. QURESHI, AND G. S. RAWAT. 2004. Effects of selective logging on vascular epiphyte diversity in a moist lowland forest of Eastern Himalaya, India. *Biol. Conserv.* 119: 81–92.
- PIGGOTT, A. G. 1988. *Ferns of Malaysia in colour*. Tropical Press, Kuala Lumpur, Malaysia.
- RICHARDSON, B. A. 1999. The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. *Biotropica* 31: 321–336.
- SCHNEIDER, H., T. A. RANKER, S. J. RUSSELL, R. CRANFILL, J. M. O. GEIGER, R. AGURAIUJA, K. R. WOOD, M. GRUNDMANN, K. KLOBERDANZ, AND J. C. VOGEL. 2005. Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proc. R. Soc. Lond. B Biol. Sci.* 272: 455–460.
- SUTTON, S. 2008. Entomology at Danum. *Antenna* 32: 29–33.
- TABERLET, P., L. GIELLY, G. PAUTOU, AND J. BOUVET. 1991. Universal primers for amplification of 3' noncoding regions of chloroplast DNA. *Plant Mol. Biol.* 17: 1105–1109.
- TANNER, E. V. J. 1980. Studies on the biomass and productivity in a series of Montane rain forests in Jamaica. *J. Ecol.* 68: 573–588.
- TREWICK, S. A., M. MORGAN-RICHARDS, I. PINTER, S. HENDERSON, S. J. RUSSELL, F. J. RUMSEY, J. A. BARRETT, M. GIBBY, AND J. C. VOGEL. 2002. Polyploidy, phylogeography and Pleistocene refugia of the rockfern *Asplenium ceterach*: Evidence from chloroplast DNA. *Mol. Ecol.* 11: 2003–2012.
- TURNER, E. C. 2005. The ecology of the Bird's Nest Fern (*Asplenium* spp.) in unlogged and managed habitats in Sabah, Malaysia. PhD Dissertation, University of Cambridge, Cambridge, UK.
- TURNER, E. C., AND W. A. FOSTER. 2006. Assessing the influence of bird's nest ferns (*Asplenium* spp.) on the local microclimate across a range of habitat disturbances in Sabah, Malaysia. *Selbyana* 27: 195–200.
- TURNER, E. C., J. L. SNADDON, T. M. FAYLE, AND W. A. FOSTER. 2008. Oil palm research in context: Identifying the need for biodiversity assessment. *PLoS ONE* 3: e1572.
- TURNER, E. C., J. L. SNADDON, H. R. JOHNSON, AND W. A. FOSTER. 2007. The impact of bird's nest ferns on stemflow nutrient concentration in a primary rain forest, Sabah, Malaysia. *J. Trop. Ecol.* 23: 721–724.
- VAN DEN HEEDÉ, C. J., R. L. L. VIANE, AND M. W. CHASE. 2003. Phylogenetic analysis of *Asplenium* subgenus *Ceterach* (Pteridophyta: Aspleniaceae) based on plastid and nuclear ribosomal ITS DNA sequences. *Am. J. Bot.* 90: 481–495.
- WALSH, R. P. D., AND D. M. NEWBERY. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rain forest regions, with particular reference to dry periods and their impact. *Philos. Trans. R. Soc. London, Ser. B* 354: 1868–1883.