

Factors Affecting the Distribution and Abundance of *Asplenium nidus* L. in a Tropical Lowland Rain Forest in Peninsular Malaysia

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ABSTRACT

Asplenium nidus is an abundant epiphytic fern of tropical rain forests in the Old World, where it plays an important ecological role in the forest canopy as host to diverse arthropod communities. We investigated the factors that determine the distribution and abundance of *A. nidus* in the canopy of an aseasonal lowland dipterocarp forest at Pasoh Forest Reserve, Malaysia. We found that *A. nidus* was more abundant in the understory, and on hosts with smooth bark and relatively flat branch angles. Ferns were found on a wide diversity and size range of host taxa. However, both host taxa and host diameter at breast height had a significant effect on *A. nidus* occupancy. *Asplenium nidus* had an aggregated spatial distribution at all scales within the study area. Spatial aggregation at larger scales appears to be driven by habitat preference, as *A. nidus* abundance was positively associated with swampy areas and negatively associated with hilly areas. At smaller scales, limited dispersal of their wind-dispersed spores most likely explains the aggregated distribution. Larger individuals occurred higher in the canopy and were more common in the hilly area. Thus, the distribution of *A. nidus* may represent a trade-off between the availability of suitable microsites for establishment in the understory and better growth conditions higher in the canopy. However, *A. nidus* is known to comprise a complex of cryptic species, and future studies should incorporate molecular techniques to elucidate the potential role of speciation in explaining these patterns.

Abstract in Malaysian is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: dipterocarp forest; epiphyte; fern; host characteristics; spatial pattern; torus test.

EPIPHYTES ARE A UBIQUITOUS COMPONENT of tropical forest canopies and provide an important resource for arthropods. *Asplenium nidus* L., commonly known as the Bird's Nest Fern, is an abundant epiphyte in tropical forests throughout the Old World (Ozanne *et al.* 2003, Ellwood & Foster 2004). This fern traps nutrients by collecting falling detritus in its leaf bases. This detritus decomposes to humus and the fern's roots push into the mulch to obtain nutrients and water. An ability to intercept detritus is nutritionally significant and for many epiphytes the detritus-capturing capacity increases with age (Reich *et al.* 2003, Karasawa & Hijii 2006a). A large individual of *A. nidus* may reach > 200 kg fresh weight (Ellwood & Foster 2004). *Asplenium nidus* also supports a high abundance and wide diversity of arthropod taxa (Basset 2001, Ellwood *et al.* 2002, Ellwood & Foster 2004, Karasawa & Hijii 2006b). A single large individual can contain up to 93 percent of the total number of invertebrates in the tree crown as a whole (Ellwood *et al.*

2002). As a result, *A. nidus* has an important ecological role in structuring rain forest arthropod communities (Karasawa & Hijii 2006c, Ellwood *et al.* 2009), particularly in lowland dipterocarp forests where epiphytes are relatively sparse.

The canopy of a tropical rain forest is characterized by steep abiotic gradients, particularly with respect to light availability and moisture levels. Young epiphytes are often prone to desiccation and thus the availability of suitable colonization microsites with soil and water trapping properties, such as branch crotches or knot-holes, may largely determine distribution patterns (Putz & Holbrook 1989, Laman 1995, Graham & Andrade 2004, Winkler *et al.* 2005). Adult plants, however, often have adaptations for storing water and nutrients, either in their tissues or, as in *A. nidus*, through structures modified to hold soil and water, and so may be less dependent on the rooting environment. Thus, microhabitat selection in epiphytes may reflect variation in the importance of different ecological filters at different stages in a plant's development. Competition, however, may not play such a significant role as epiphyte populations are commonly thought to be dispersal limited (Ackerman *et al.* 1996, Laman 1996, Cascante-Marin *et al.* 2009). Studies have shown that tropical

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epiphytes often prefer particular hosts and occupy specific positions within the canopy with respect to the height aboveground and position along the branch (Zimmerman & Olmsted 1992, Hietz & Hietz 1995, Harrison *et al.* 2003, Laube & Zotz 2006, Zotz & Schultz 2008). Previous studies on *A. nidus* have shown that drought is an important factor in structuring populations and prolonged droughts may kill a large proportion of the individuals in a forest (Freiberg & Turton 2007); however, *A. nidus* is an abundant fern in aseasonal lowland rain forest and occurs throughout the vertical structure of the forest (Ellwood & Foster 2004).

The aim of this study was to identify the factors that affect the distribution and size of *A. nidus* in the canopy of an aseasonal lowland rain forest. We hypothesized that (1) host trees of *A. nidus* would have particular characteristics, such as rough bark, flat branches, and large size; (2) *A. nidus* would have a preference for swampy areas, because of improved survival prospects in more humid conditions (Freiberg & Turton 2007); and (3) larger *A. nidus* would be found higher in the canopy, because of increased light levels.

METHODS

STUDY SITE AND METHODS.—The study area was located within the Pasoh Forest Reserve (2°58' N, 102°18' E), ca 70 km southeast of Kuala Lumpur. The overall vegetation type in this reserve is lowland dipterocarp forest (Kochummen *et al.* 1990). In 1985, a 50 ha plot Forest Dynamics Plot was established by the Forest Research Institute Malaysia (FRIM) and the Center for Tropical Forest Research in the primary forest at Pasoh Forest Reserve (Kochummen *et al.* 1990). Our study was conducted in the 50 ha plot from 14 to 19 August 2008.

We established 10 transects of 40 m width and 1000 m length, along the entire length of the 50 ha plot. The transects thus covered a 40 ha area, from the northwest (0, 500 m) to the southeast side of the plot (1000, 100 m). This area incorporated the full variation in topography and soil types found within the plot. The position of all trees and lianas in the plot were previously mapped and tagged. We located all tree individuals used by *A. nidus* and recorded the tag number, bark type (smooth, scaly, fissured, cracked), branch angle

(< 30°, 30–60°, > 60°), and canopy position (emergent, canopy, understory). Tag data were used to identify the position and diameter at breast height (dbh) of the host trees from the plot dataset. We also recorded the number of individuals of *A. nidus* on a host, estimated the size of the fern base, measured the height from the ground of each *A. nidus* individual using a clinometer, and noted the position on the tree (branch or trunk).

DATA ANALYSIS.—To examine the affect of host taxa and host dbh on *A. nidus* occurrence we used a binomial model (fern present/absent) using all the trees ≥ 11 cm dbh as the universe of potential hosts. The smallest host occupied by *A. nidus* in our survey was 11 cm dbh. We used multi-regression analysis to examine the effect of host characteristics on fern size. In both cases, we started with the maximal model and used stepwise simplification and AIC to select the best model.

We used the torus-translation test to analyze the association between *A. nidus* and topography/soil types. This analysis, a type of randomization test, was introduced by Harms *et al.* (2001) in measuring habitat association of trees and shrubs in a 50 ha Neotropical forest plot. It limits the problem of spatial autocorrelation of habitats by rotating the habitat map beneath the tree map.

In addition, Ripley's *K* statistic was used to measure the spatial point pattern of *A. nidus* within the study area. The *K* statistic computes the density of *A. nidus* within a distance *r* from an individual, averaged over all individuals. To quantify clumping, we compared the observed *K* values with a null hypothesis of complete spatial randomness (Plotkin *et al.* 2002), and 95% confidence envelopes for the spatial randomness null hypothesis were calculated. All data were analyzed using R v2.8.0 (package 'spatstat'; R Development Core Team 2009).

RESULTS

We found 169 individuals of *A. nidus* (Fig. 1) on 123 host trees. Twenty-eight host trees had > 1 *A. nidus* individual. One *Kenema scortechinii* (Myristicaceae) had 6 individuals; the highest number recorded on a single host. *Asplenium nidus* were predominantly

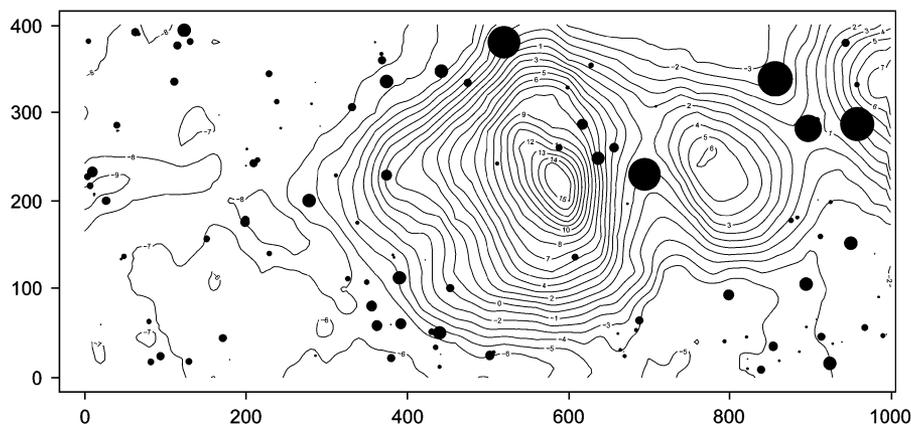


FIGURE 1. Spatial distribution of *Asplenium nidus* over 40 ha of the Pasoh plot. The size of the circles indicates the relative size of *A. nidus* individuals.

TABLE 1. The percentage frequency of different host characteristics among 123 *Asplenium nidus* host trees, including bark type, average branch angle, and canopy stratum.

Tree characteristics	%
Bark type	
Smooth	65.0
Cracked	9.76
Fissured	16.3
Scaly	9.47
Average branch angle	
0–30°	10.7
30–60°	44.6
> 60°	44.6
Canopy stratum	
Emergent	12.2
Canopy	24.4
Understory	63.4

found on understory trees (63.4%) with smooth bark (65.0%) and medium to flat branch angles (89.2%) (Table 1).

The 123 host trees included 95 species in 67 genera and 29 families (Table 2). Thus, *A. nidus* occupied a diversity of hosts at all taxonomic levels. As suggested by their abundance in the understory, *A. nidus* occupied mostly smaller trees (100–200 mm dbh; Fig. 2). Nevertheless, both host species and host dbh had a significant effect on host occupancy by *A. nidus* (Table 3). Model simplification resulted in three groups of species; one that was negatively associated with *A. nidus* occupancy, one that was strongly associated with *A. nidus* occupancy, and an intermediate group. Species most strongly associated with *A. nidus* occupancy included, *Teijsmanniodendron simplicifolium* (Verbenaceae), *Sapium baccatum* (Euphorbeaceae), *Syzygium leptostemon* (Euphorbeaceae), *Beilschmiedia dictyoneura* (Lauraceae), and *Antidesma coriaceum* (Euphorbeaceae). Although highly significant, the effect of host dbh was weak (Table 3).

From the torus-translations test, we found there was a strong association between *A. nidus* and topography. *Asplenium nidus* was negatively associated with hilly topography ($P < 0.01$) and positively associated with flat areas ($P < 0.01$). Soil type is strongly

TABLE 2. Percentage frequency of the five most common genera and families among 123 host trees of *Asplenium nidus*.

Genus	%	Family	%
<i>Syzygium</i>	7.32	Euphorbiaceae	13.0
<i>Kenma</i>	5.69	Dipterocarpaceae	10.6
<i>Shorea</i>	4.88	Myrtaceae	8.94
<i>Aidia</i>	4.07	Myristicaceae	7.32
<i>Diospyros</i>	4.07	Rubiaceae	7.32

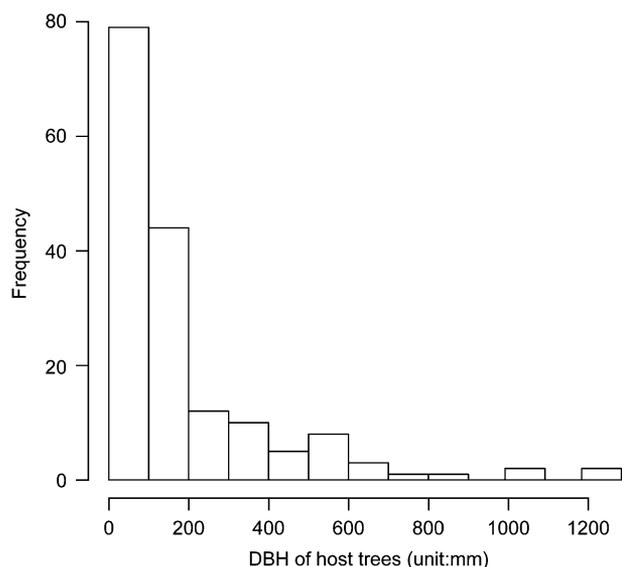


FIGURE 2. A frequency distribution of *A. nidus* host tree dbh.

correlated with topography at Pasoh, with shales dominating the hilly area and alluvium in the flat areas (Okuda *et al.* 2003).

An analysis of Ripley's K statistic indicated that *A. nidus* had an aggregated distribution at all spatial scales measured (Fig. 3). The broken lines indicate the expected number of *A. nidus* and its 95% confidence envelope under an assumption of complete spatial randomness. The observed curve lies above the confidence envelope at all distances indicating spatial aggregation at all spatial scales.

We used a multiple-regression analysis to identify the factors affecting the size of *A. nidus* individuals. We found that *A. nidus* size was strongly influenced by the host species, height above-ground, and host average branch angle ($F_{5,161} = 87.4$, $P < 0.0001$; Table 4); the higher the position of *A. nidus* from the ground, the larger their size. The largest *A. nidus* (base diam 1300 mm) was found on a *Shorea ovalis* (Dipterocarpaceae) host with a dbh of 710 mm. Comparing the size of *A. nidus* from the hilly area and flat area, we found that *A. nidus* in the hilly area were larger (Wilcoxon rank-sum test with continuity correction, $W = 2354$, $P = 0.0009$).

DISCUSSION

The dependence of one life form on another for physical support is a common phenomenon in the tropics. Indeed, the most common form of several large families is epiphytic (Ewel & Hiremath 2005). Microhabitat selection by epiphytes is likely to be influenced by host characteristics, as these influence an epiphyte's ability to obtain water, nutrients, and light. In this study we found that most of the trees used by *A. nidus* had smooth bark, relative flat branches, and understory canopies. The high proportion of hosts with smooth bark may simply reflect a higher proportion of smooth-barked trees in the understory. Intuitively, relatively flat branch angles provide a suitable platform for *A. nidus* to perch on, particularly as they get larger. Meanwhile, the prevalence of *A. nidus* in the understory may

TABLE 3. Results of a binomial model of host occupancy by *Asplenium nidus* ($\text{Occupancy} \sim \text{Host dbh} + \text{Host Species}$, Res. Dev. = 1643, $df = 250779$). Species groups 1–3 were the groupings of host tree species obtained through model simplification.

Effect	Estimate	SE	Z	P
(Intercept)	-9.9706250	0.2631049	-37.9	< 0.00001
dbh	0.0053295	0.0002872	18.6	< 0.00001
Species group 2	2.3776227	0.4544689	5.23	< 0.00001
Species group 3	3.5453263	0.2696808	13.1	< 0.00001

reflect the higher humidity and lower levels of direct sunlight lower in the canopy, and thus a greater abundance of suitable microsites for the establishment of juvenile plants. Freiberg and Turton (2007) suggested moisture availability was important in determining the distribution of *A. nidus*. A drought of 4 wk was sufficient to completely dry the humus trapped in even large ferns, while a prolonged drought of 2 mo or more was sufficient to kill them (Freiberg & Turton 2007). *Asplenium nidus* occupancy, however, was positively correlated with host dbh, suggesting that the abundance in the understory may simply reflect the greater number of hosts in this size class. Future studies could investigate these factors through controlled field experiments.

Asplenium nidus had an aggregated distribution at all spatial scales measured. Many papers have pointed out that both dispersal limitation and habitat differentiation can contribute to spatial aggregation (Plotkin *et al.* 2002). From our habitat analysis, *A. nidus* was found to prefer the flatter, swampy areas of the plot suggesting that at larger spatial scales the aggregated pattern may be driven by habitat preference. As with the occurrence of plants in the canopy, this habitat preference of *A. nidus* may reflect higher humidity and an increased abundance of suitable microsites for juvenile survival in the swampy areas. At smaller scales, spatial aggregation of *A. nidus* may be explained by dispersal limitation. *Asplenium nidus* reproduces by spores, which are primarily dispersed by wind, and most *A. nidus* occurred in the understory, where air currents are weak, limiting the capacity for long-distance dispersal. Many host trees had > 1 *A. nidus* individual, further suggesting dispersal is limited.

As with most plants, size is an important characteristic for *A. nidus*, because larger ferns can hold more soil and water. Fern size was strongly correlated with host taxa, average branch angle, and height above the ground. The larger size of individuals higher in the canopy may reflect better growth conditions, where light is most abundant. The distribution of *A. nidus* may therefore reflect a trade-off between better light conditions higher in the canopy, but a higher abundance of suitable microsites for juvenile establishment and survival lower in the canopy. Such trade-offs may be a common feature of epiphyte ecology (Harrison *et al.* 2003, Winkler *et al.* 2007). It is also possible that higher *A. nidus* were larger, simply because older individuals had been lifted into the canopy by the growth of their host. Large *A. nidus*, however, may not be very old

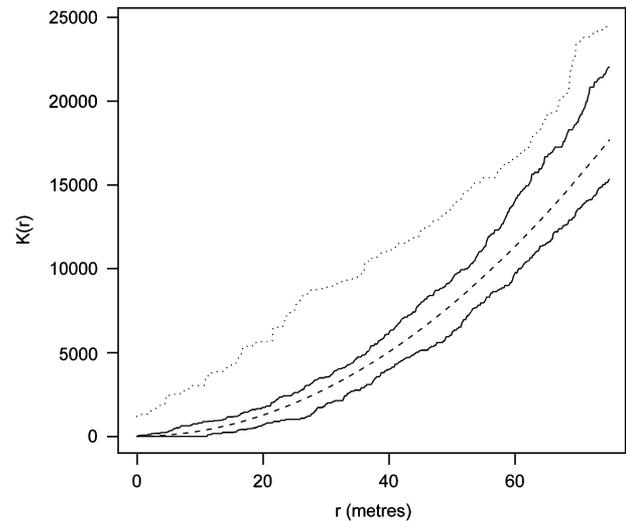


FIGURE 3. Ripley's K statistic for the spatial point pattern of *Asplenium nidus* in the Pasoh plot. The dotted line is the observed distribution, and the two solid lines and dashed line represent the simulated distributions based on complete spatial randomness; the solid lines form the 95% confidence envelope of the simulation distribution.

(Freiberg & Turton 2007). The distribution pattern is significant for the arthropods that depend on *A. nidus*, because size and canopy height were found to be important factors in structuring the arthropod community (Ellwood *et al.* 2009).

An alternative explanation for these patterns is that the large-canopy ferns and small-understory ferns are actually different cryptic species. In Indonesia at least two cryptic species of *A. nidus* were found coexisting in the same habitat (Yatabe *et al.* 2001). Large ferns were also more prevalent in the hill habitat, although the swampy habitat had a greater total abundance of ferns, which tends to support this conjecture. Future experimental studies combining ecophysiology and molecular genetics may resolve these questions

TABLE 4. Results of a multi-regression model employed to identify the factors affecting the size of *Asplenium nidus* ($\text{adj. } R^2 = 0.723$, $F_{5, 161} = 87.4$, $P < 0.00001$). Species groups 1–3 were the groupings of host trees species obtained through model simplification. Height, height of *A. nidus* above ground. Branch angle was classified into one of three classes (< 30°, 30–60°, > 60–90°), based on the average class for the primary branches (those coming directly off the trunk).

Effect	Estimate	SE	F	P
(Intercept)	60.4158	5.0571	11.9	< 0.00001
Species group 1	-69.2246	12.0628	-5.74	< 0.00001
Species group 2	-48.1236	3.2520	-14.8	< 0.00001
Species group 3	-35.0774	3.4228	-10.2	< 0.00001
Height	0.9347	0.1214	7.70	< 0.00001
Average branch angle	-3.9510	1.3983	-2.83	0.00532

and provide an understanding of the evolution of the *A. nidus* species complex.

Global climate change models suggest that tropical Asia will experience increased rainfall overall, but in seasonal areas dry seasons will become more severe (Corlett 2009). Previous work has shown that even large *A. nidus* individuals are killed by severe drought (Freiberg and Turton 2007), and our findings are consistent with the notion that the distribution of *A. nidus* within the forest is largely determined by moisture availability. Thus, if the predictions of the climate models are borne out, we can expect that the range of *A. nidus* outside the core-aseasonal centre of SE Asia will decline, and where they occur they will be restricted to the wetter habitats and understorey to a greater extent. Within the aseasonal zone, inter-annual variation in rainfall is critical (Harrison 2001), but here the predictability of current climate models fails (Corlett 2009). Nevertheless, the sensitivity of *A. nidus* to droughts could make it a useful indicator of climate change, where local meteorological data are lacking.

Asplenium nidus was more frequent on host trees with particular characteristics, such as understory trees with smooth bark and flatter branches. It had an aggregated distribution at all scales within the study area, possibly as a result of dispersal limitation at small spatial scales and a preference for swampy areas of the plot at larger spatial scales. Larger individuals occurred higher in the canopy and were more prevalent in the hill habitat suggesting a possible trade-off between conditions suitable for juvenile survival and adult growth. Future studies should investigate the role of cryptic speciation in determining these patterns.

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