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SHORT COMMUNICATION

Mortality and recruitment of hemi-epiphytic figs in the canopy of a Bornean rain forest

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Hemi-epiphytic figs (Moraceae; *Ficus* subgenus *Urostigma*) are a distinctive component of the canopy of tropical rain forests. The hemi-epiphytic habit has risen independently several times, and is recorded in over 20 plant families today, but with approximately 350 species globally figs are by far the most important (Berg & Corner 2005, Putz & Holbrook 1986). They are ubiquitously diverse in tropical lowland rain forests and are represented by independent radiations in each region (Harrison 2005, Jousselin *et al.* 2003). Moreover, their abundant production of fruit at all times of the year makes them functionally important as food for wildlife, especially during periods of general fruit shortage (Shanahan *et al.* 2001a). However, hemi-epiphytic fig populations occur at very low densities and this, combined with the difficulties of access to the canopy, has meant that study of their biology lags behind that of other rain forest plants (Harrison *et al.* 2003). Here, I present the first estimates of mortality and recruitment for any community of hemi-epiphytic figs.

Hemi-epiphytic figs colonize a huge diversity of tree species in tropical rain forests and, although some associations with particular host taxa or bark types have been reported in species-poor forests, by far the most significant factor is host size (Compton & Musgrave 1993, Daniels & Lawton 1991, Doyle 2000, Harrison *et al.* 2003, Laman 1996a, Male & Roberts 2005, Michaloud & Michaloud 1987, Patel 1996). Moreover, two independent studies in Borneo found evidence for specialization among hemi-epiphytic fig species for hosts in different canopy strata (Harrison *et al.* 2003, Laman 1996a). Many species appear to have stringent microsite requirements for germination and seedling survival in the canopy (Holbrook & Putz 1996, Laman 1995, Swagel *et al.* 1997) and, despite extraordinary fecundity, few seeds appear to reach suitable sites (Laman 1996b). There is substantial variation in growth form among hemi-epiphytic figs. Banyans have abandoned the hemi-epiphytic habit altogether and root directly in the ground or are lithophytic. This growth form is, however, absent from tropical rain forests and, in fact, some species that occur as hemi-epiphytes in the forest are facultative banyans in littoral forest or other open environments (Corner 1988, Shanahan *et al.* 2001b). Among species that are true hemi-epiphytes most remain dependent on their hosts. However, stranglers, as their name suggests, kill their hosts. This involves a much greater investment in aerial roots, as these must ultimately support both the fig and dead host, but the plant gains from an improved light environment and escapes the risk of mortality from the host tree-fall (Harrison *et al.* 2003). Growth rates of hemi-epiphytic figs have never been measured, but they are presumably very high in some species as huge individuals can sometimes be found engulfing abandoned buildings (Perry & Merschel 1987).

In February–March 1998 the hemi-epiphytic figs in two tree plots (total 60 ha) at Lambir Hills National Park (Lambir; 4°20′N 113°50′E, 150–250 m asl), Sarawak, Malaysia were surveyed (Harrison *et al.* 2003). In both these plots all trees (>1 cm dbh in a 52-ha plot, >10 cm in an 8-ha plot) have been individually tagged, measured and identified (Lee *et al.* 2002, Nakagawa *et al.* 2000). All hemi-epiphytic figs with an aerial root connected to the ground were recorded (maximum size of epiphytic seedlings is approximately 1 m height, *pers. obs.*). Allometric models are not available for the hemi-epiphytic growth-form, so I estimated fig size by taking the diameter of the aerial root at breast height and assessed crown area by measuring four radii at roughly 90° with a tape measure on the ground. Species that were strictly hemi-epiphytic had aerial roots ranging in diameter from

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0.3 cm to 28.0 cm (mean = 5.98 cm, SD = 5.65 cm), and crown area (m^2) scaled with aerial root diameter according to the equation; area = 38 + 35.4 diameter (intercept SE = 22.6, coefficient SE = 2.75, $r^2 = 0.518$). For the one strangler species aerial root diameter ranged from 2.0 cm to 130 cm (mean = 46.5 cm, SD = 44.2 cm), and crown area scaled with aerial root diameter according to the equation; area = 411 + 9.6 diameter (intercept SE = 183, coefficient SE = 2.90, $r^2 = 0.497$). However, these crown area estimates have to be treated with caution as hemi-epiphyte canopies are often disconnected, with individual branches sticking out from different sides of the host crown, making them difficult to assess. For this reason I use aerial root diameter as the estimate of fig size in all subsequent analyses. The plots were re-censused for hemi-epiphytic figs in December 2005 to ascertain whether the earlier recorded individuals were dead or alive, to determine causes of death, and to record recruits. Mortality (M) and recruitment (R) were calculated using the formulae:

$$M = \left(1 - (1 - D/X)^{1/n}\right) \times 100$$

and

$$R = \left(1 - (1 - C/X)^{1/n}\right) \times 100,$$

where X equals the initial number of individuals sampled, D and C equal the number of dead trees and new recruits, respectively, and n equals the length of the interval in years (Nakagawa *et al.* 2000, Shiel & May 1996). Given the unusually long census interval (7.75 y), a number of individuals may have colonized and subsequently died leading to under-estimates of recruitment and mortality among smaller individuals (Lewis *et al.* 2004).

Of 182 hemi-epiphytic fig individuals recorded in 1998, 57 were dead by 2005 (Table 1), a mortality rate across species of 4.73% y^{-1}. Among the five species with sufficient sample sizes to make separate estimates there was no significant difference in mortality rates ($\chi^2 = 0.964$, df = 4, P = 0.915). By far and away the most important cause of death was host tree-fall, accounting for 74% of the mortality (Table 1). Of the 15 individuals that died from other causes most died on their hosts. However, three individuals died when their host was struck by a neighbouring tree, two were killed by a large landslide, and one individual was a free-standing strangler. Death from host tree-fall was independent of either the size of the fig (logistic regression, odds ratio = 0.998, 95% CI of odds ratio 0.978–1.018, model $\chi^2 = 0.040$, df = 1, P = 0.842) or the size of the host (logistic regression, odds ratio = 1.006, 95% CI of odds ratio 0.994–1.018, model $\chi^2 = 0.911$, df = 1, P = 0.340). However, smaller individuals were significantly more likely to die on their hosts than larger ones (logistic regression, odds ratio = 1.481, 95% CI of odds ratio 0.937–2.340, model $\chi^2 = 7.32$, df = 1, P = 0.007). An increase in aerial root diameter of 5 cm decreased the likelihood of dying on the host by a factor of seven. Trees in the 52-ha plot were censused in 1997 and again in 2003. Over this period, trees (>10 cm dbh) with a hemi-epiphytic fig were significantly more likely to fall than those that did not support a fig (15.3 vs. 8.9%) (Fisher's exact test, one-tailed, $\chi^2 = 6.032$, P = 0.009). Only 18 hemi-epiphytic fig recruits were observed (1.33% y^{-1}); just 32% of the number of figs that died over the same period (Table 1).

Table 1. Mortality and recruitment of hemi-epiphytic figs (*Ficus* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. Taxonomic arrangement follows Berg & Corner (2005). N = original number of individuals surveyed (60 ha) in January–March 1998; M = total mortality to December 2005; R = total number of individuals recruited to December 2005.

			Cause of death		
Species	N	M	Host tree-fall	Other	R
Section *Urostigma*					
F. caulocarpa Miq.	1	0	–	–	0
F. virens Ait.	1	1	1	–	0
Section *Conosyce*					
Subsection *Conosyce*					
F. consociata Bl.	5	3	3	–	0
F. cucurbinita King	5	0	–	–	1
F. drupacea Thunb.	1	0	–	–	0
F. kerkhovenii Val. (hemi-epiphyte)	12	4	3	1	1
F. kerkhovenii Val. (free-standing)	5	1	–	1	0
F. paracamptophylla Corner	18	4	1	3	2
F. cf. *annulata*	1	0	–	–	0
F. stupenda Miq.	7	2	2	–	1
F. subgelderi Corner	27	9	8	1	3
F. subtecta Corner	2	1	–	1	0
F. xylophylla Wall. ex Miq.	21	6	5	1	1
Subsection *Dictyoneuron*					
F. binnendykii Miq.	3	0	–	–	0
F. soepadmoi Kochummen	7	2	1	1	3
F. delosyce Corner	25	9	8	1	2
F. dubia Wall. ex King	13	3	3	–	0
F. pellucido-punctata Griff.	4	2	2	–	0
F. pisocarpa Bl.	4	1	1	–	0
F. retusa L.	6	2	1	1	1
F. spathulifolia Corner	2	0	–	–	1
Subsection *Benjamina*					
F. benjamina L.	1	1	1	–	0
F. callophylla Bl.	1	1	–	1	0
F. subcordata Bl.	5	1	1	–	0
Unknown	5	4	1	3	2
Total	182	57	42	15	18

At over 4.7% y^{-1} the mortality of hemi-epiphytic figs is very high compared to trees at Lambir. Although higher rates may be recorded for brief periods during severe droughts (Nakagawa *et al.* 2000, Potts 2003), background mortality rates for trees over 10 cm dbh vary from approximately 1% y^{-1} to 2.5% y^{-1} depending on the soil type (Potts 2003, Russo *et al.* 2005). Combined with the fact that the main source of mortality, that from host tree-fall, was independent of either fig or host size, this suggests that population turnover is high among hemi-epiphytic figs and that individuals are not long-lived, despite their large size. Smaller individuals were more likely to die on their host (dead individuals ranged 1–6 cm aerial root dbh) suggesting figs are vulnerable until their aerial roots are well established. Earlier studies found some association between hemi-epiphytic fig distributions and soil or topographic variables (Harrison *et al.* 2003, Laman 1996a). Differential mortality during the phase of aerial root establishment may be responsible for these patterns. The fact that trees supporting a hemi-epiphytic fig were more likely to fall than those that did not have a fig is interesting. It indicates that the hemi-epiphytic figs may be weakening their hosts in some way, although obviously this is not to the selective advantage of the fig. Increased wind resistance in the canopy would appear to be the most likely cause, although other factors such as weakened root systems through competition for resources or asymmetric loading of the host trunk through unequal growth of the fig crown may play a part. It is also possible that hemi-epiphytic figs preferentially colonize overly mature trees, if these offer more suitable microsites for seedling establishment, such as notches with rotten wood or more open crowns as a result of fallen branches. However, as many of the figs that were killed by host tree-fall were large, their hosts must be surviving for substantial periods following the establishment of the epiphytic fig seedling. The lack of a relationship between mortality caused by host tree-fall and fig size is curious, as one would expect the effects of factors such as wind resistance, competition, and asymmetric loading to increase with fig size. Various causes of host tree-fall may be important at different stages in the growth of a hemi-epiphyte. Or the lack of a relationship may simply be an artefact of averaging across species that colonized hosts of various sizes in different canopy strata. The high mortality rate caused by host tree-falls illustrates clearly the advantages of the strangling habit, which has arisen independently several times among hemi-epiphytic figs (Harrison *et al.* 2003).

The fact that the recruitment rate was so much lower than the rate of mortality is also noteworthy. This may be partly due to observational bias, but the proficiency of the observers is sufficient that this is unlikely to be a major factor. Low recruitment rates may reflect the fact that seed disperser populations, in particular hornbills, primates and flying foxes, are very depressed in Lambir as a result of hunting (Shanahan & Debski 2002). Indeed several larger vertebrate species have been extirpated from the park, and the crops of some hemi-epiphytic figs, especially those with larger fruit, are often poorly dispersed (*pers. obs.*). These figs are importance sources of food for other animals in the forest, and so to the forest as a whole for their maintenance of the seed disperser community (Shanahan & Compton 2001). Thus if substantiated, this may indicate the start of cascading effects resulting from over-hunting, as conservation biologists have long predicted (Primack & Corlett 2005). A comparison with an area that still has an intact seed disperser community is required, and to preserve the forest at Lambir greater efforts should be made to stem hunting.

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