THE ROYAL SOCIETY

# Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo

**Rhett D. Harrison**

*Centre for Ecological Research, Kyoto University, Kamitanakami Hirano-cho, Otsu 520-2113, Japan* (*rhett@ecology.kyoto-u.ac*)

Figs (*Ficus* spp.) and their species-specific pollinators, the fig wasps (Agaonidae), have coevolved one of the most intricate interactions found in nature, in which the fig wasps, in return for pollination services, raise their offspring in the fig inflorescence. Fig wasps, however, have very short adult lives and hence are dependent on the near-continuous production of inflorescences to maintain their populations. From January to March 1998 northern Borneo suffered a very severe drought linked to the El Niño–Southern Oscillation event of 1997–1998. This caused a substantial break in the production of inflorescences on dioecious figs and led to the local extinction of their pollinators at Lambir Hills National Park, Sarawak, Malaysia. Most pollinators had not recolonized six months after the drought and, given the high level of endemism and wide extent of the drought, some species may be totally extinct. Cascading effects on vertebrate seed dispersers, for which figs are often regarded as keystone resources, and the tree species dependent on their services are also likely. This has considerable implications for the maintenance of biodiversity under a scenario of climate change and greater climatic extremes.

**Keywords:** biodiversity; drought; extinction; *Ficus*; fig wasp; keystone species

## 1. INTRODUCTION

The lowland dipterocarp forests of South-East Asia are the oldest and most diverse rainforests on Earth. Their antiquity and the favourableness of a permanently humid, equatorial climate with little seasonality has been implicated in the development of such high biological diversity (Whitmore 1984). Nevertheless, occasional droughts are considered to have a major impact on the ecology of these forests (Whitmore 1984, 1998; Ashton 1993; Walsh 1996), especially through increased tree mortality caused by water stress (Becker *et al.* 1998; Tyree *et al.* 1998) and largely anthropogenic fires (Leighton & Wirawan 1986; Woods 1989). The response of animal populations, such as the herbivores, pollinators or seed dispersers that are directly dependent on plant resources, to these catastrophic disturbances is hardly known. Although, with increasing isolation of populations into small relic patches of forest, the possibility of a gradual loss of biodiversity and even ecosystem collapse if coevolved interactions disintegrate has been recognized (Whitmore 1998). Recent predictions of worsening and more frequent drought induced by global warming (Meehl 1997; Guilderson & Schrag 1998; Salafsky 1998; Timmermann *et al.* 1999) are therefore of serious concern.

The figs (*Ficus* spp.) are one of the most diverse and ecologically important genera in lowland dipterocarp forests (Corner 1988; Lambert & Marshall 1991). Figs have a closed urn-shaped inflorescence, or syconium, lined with tiny uniovulate flowers. Species-specific pollinating wasps (Hymenoptera: Agaonidae) enter the syconium through a narrow, bract-covered passage, losing their wings in the process, pollinate the flowers and attempt to oviposit. Ovules that receive a wasp egg form a gall on which the wasp larvae feeds, while others if pollinated develop into a seed in the normal way. Several weeks later adult wasps emerge and mate within the syconium. The wingless males then die, while the females collect pollen and depart in search of receptive syconia. In dioecious figs, trees are either functionally male, and adapted for the production of wasps and pollen, or female and produce seed. Wasps can only reproduce in the male syconia. Female syconia mimic those on male trees so that the wasps enter and pollinate but are unable to oviposit. Hence, they die without reproducing (Galil 1973). In most species a suite of related non-pollinating wasps, usually detrimental to the fig's reproductive success, also raise their offspring in the syconia (West & Herre 1994; Kerdelhue & Rasplus 1996*b*).

Adult female pollinators have an extremely short life span (approximately one day; Kjellberg *et al.* 1988; R. D. Harrison, unpublished data). Thus, within a population of fig trees the cycling of the pollinator population from one crop to the next can only be maintained if syconia production is nearly continuous. Consequently, figs are restricted to habitats, or climates, where this is possible. It is also the continuous production of fruit, especially when there is a dearth of other seasonal fruits, that makes figs so valuable to vertebrate seed dispersers (Terborgh 1986; Lambert & Marshall 1991).

The unprecedented El Niño–Southern Oscillation (ENSO) event of 1997–1998 (Webster & Palmer 1997) induced the longest drought on record for north-western Borneo (figure 1), considerably more severe than that caused by the 1982–1983 ENSO which previously held this accolade (Leighton & Wirawan 1986; Woods 1989). Large areas of northern Borneo, including north Sarawak, Brunei, Sabah, and parts of Kalimantan, experienced widespread fires and a haze crisis. As in the 1982–1983 ENSO (Leighton & Wirawan 1986; Woods 1989), drought killed many mature trees (Nakagawa *et al.* 2000). Out of 576 individuals in 305 plant families under phenological observation at Lambir Hills National Park (LHNP, 4°20′ N, 113°50′ E, 50–250 m above sea level), only 29 individuals died over a five-year period between January 1993 and January 1998, mostly from tree falls,

 
*Received* 2 September 1999 *Accepted* 19 November 1999

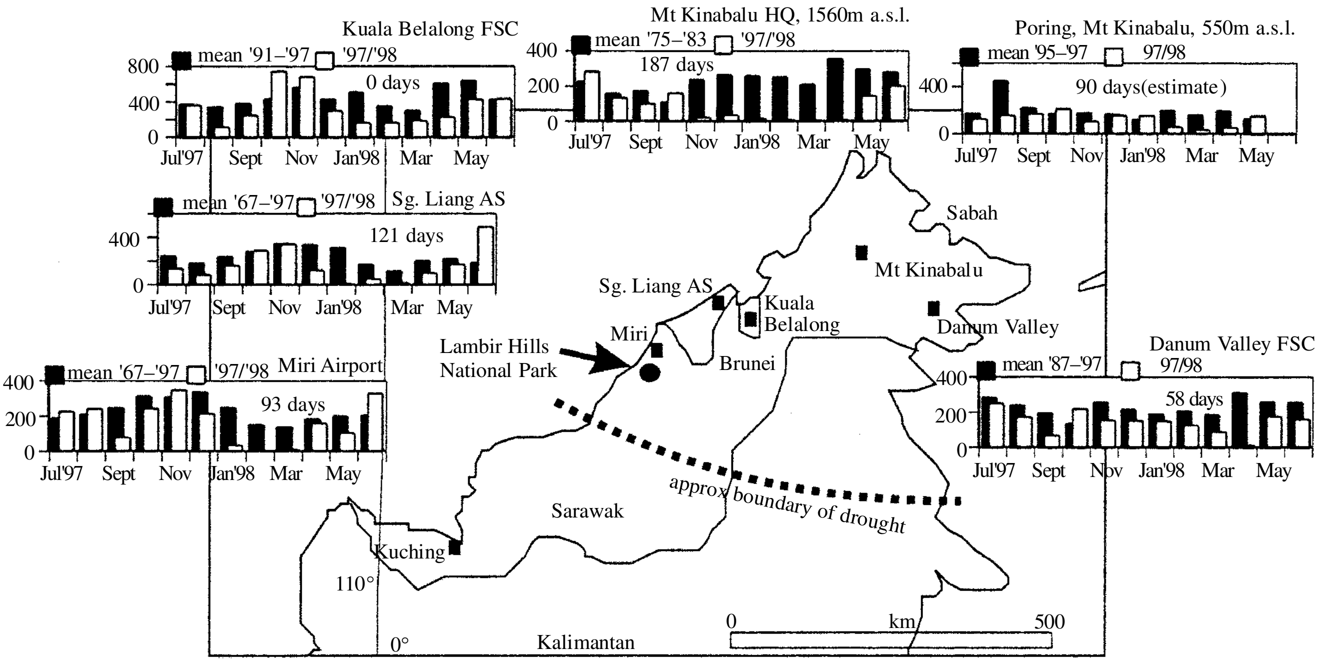


Figure 1. Map of northern Borneo showing the area affected by the 1998 drought. For each of the six sites monthly rainfall (millimetres) from July 1997, the start of the ENSO, to June 1998 is compared to the long-term monthly means. The number of days for which the 30-day rolling rainfall totals remained below 100 mm is also given (mean monthly evaporation is *ca*. 100 mm; Whitmore 1984). From January to March 1998 only 7% of the mean rainfall over the same three months fell at LHNP. Comparison to published accounts of long-term rainfall records from Miri indicate that this was the worst drought since records began or at least in 70 years, and a drought of such severity would be expected less than once in 350 years (Nakagawa *et al*. 2000; Harrison 2000).

but a further 63 died during 1998 (Canopy Biology Program Sarawak; R. D. Harrison, unpublished data). Drought can be presumed to be the main cause as other large-scale factors, such as fire, wind throw or insect attack, can be ruled out. On the summit of Mt Kinabalu, the only other site with published observations of the 1998 drought thus far, a very high mortality across all types of vegetation was recorded, again suggesting the impact was more severe than in previous droughts and also demonstrating that it affected a wide geographical area and altitudinal range (Kudo & Kitayama 1999).

## 2. MATERIAL AND METHODS

Observations of fig phenology in LHNP started in October 1994, and from March 1997 to October 1998 25 species of dioecious fig and 12 species of monoecious fig were included in the phenology census (the species identification followed was from Corner (1965)). However, for many species the sample sizes were small, often only one or two mature individuals, as reflected their densities in and around the national park. Censuses were conducted approximately every ten days and at each census the leaf and syconia phenology were recorded. The total number (log scale with three subdivisions) and proportion at each developmental stage (immature, receptive, pollinated, male–fruit (Galil 1973)) of syconia were assessed. For species with accessible syconia, including one climber (*F. punctata*) for which ladder systems were used, the crop stage could be assessed directly by sampling and opening or by inspection of the external appearance and evidence such as pollinator wings in the ostiole bracts. For most climbers and hemi-epiphytes with inaccessible syconia the developmental stage was assessed through binoculars, which cannot be considered reliable for short phases such as the receptive and wasp-producing phases, but was sufficient to recognize immature, mid- to late-stage pollinated and fruit phases.

PROC SUMMARY in SAS (SAS Institute, Inc. 1985) was used to generate total numbers of syconia at each crop stage for each species by census. This paper deals only with the impact of the severe drought in 1998 on the fig wasp populations.

## 3. RESULTS

The number of pollinated syconia is indicative of the presence of adult pollinators at the time of crop receptivity and the population size of wasp larvae developing on the trees (males only for dioecious figs) under observation. Figure 2 shows the number of pollinated syconia on eight selected species of (*a*) dioecious and (*b*) monoecious figs from January 1997 to October 1998, when observations ceased. The numbers of pollinated syconia on dioecious figs, though variable in some species and/or sexes reflecting the initiation of syconia, indicate that the pollinator populations were stable up until the beginning of the drought in January 1998. However, all pollinators of these figs were locally extinct by the end of March 1998, two and a half months after the onset of dry conditions (figure 2*a*). Trees dropped leaves, failed to initiate new syconia, and even pollinated syconia withered. The gap this caused in the availability of receptive syconia was over two months in these species, or approximately twice the total life span of the pollinators. The non-pollinating wasp communities of these figs, some of which can retain

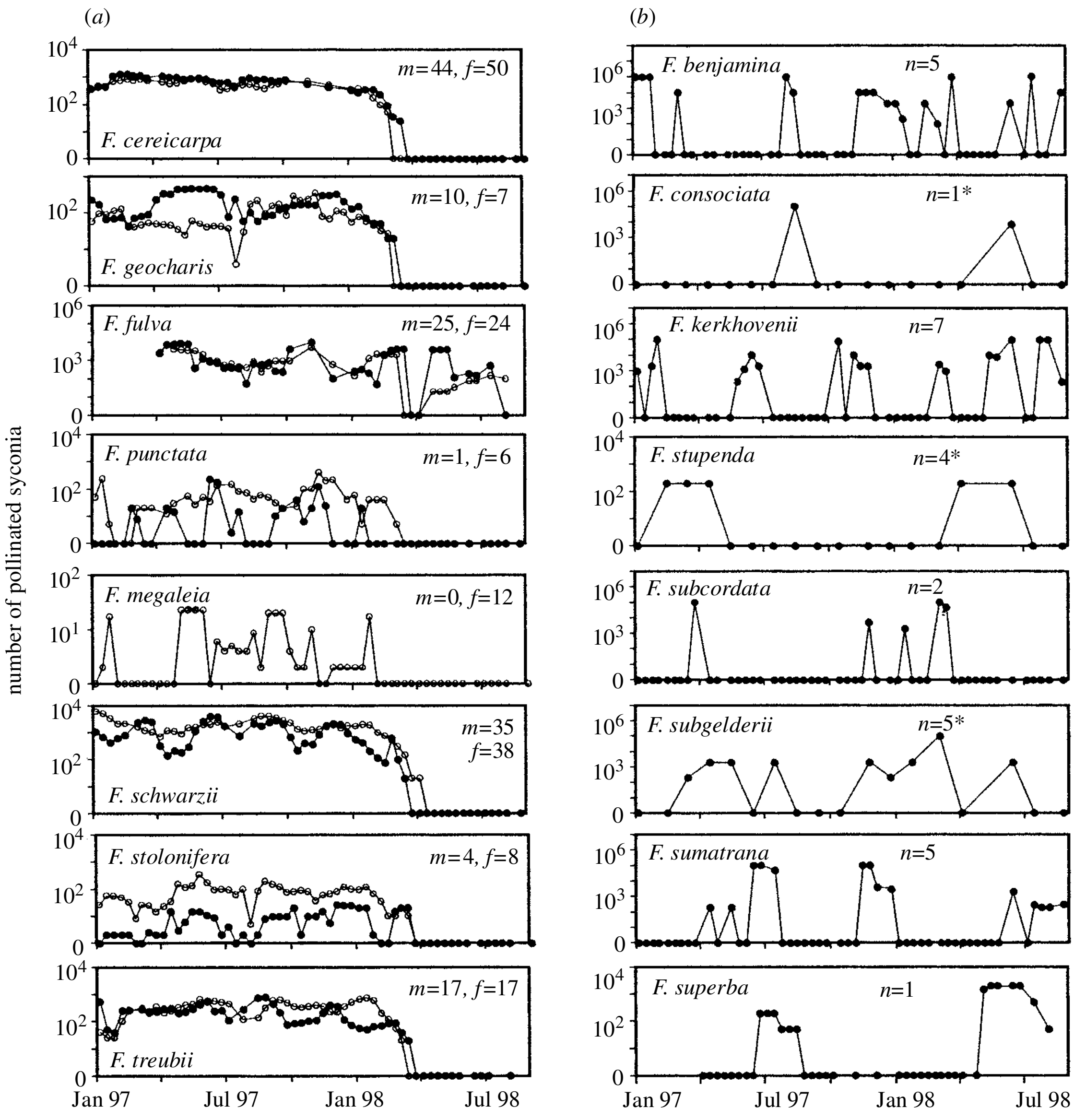


Figure 2. Number of pollinated syconia at each census on (*a*) dioecious (filled circles, male trees (*m*), open circles, female trees (*f*)), and (*b*) monoecious figs at LHNP. Pollinated syconia are indicative of (i) the presence of pollinating wasps at the time of crop receptivity, and (ii) the population of wasp larvae developing within the observed fig population, male trees only for dioecious figs. If syconia are not pollinated they are eventually aborted. Phenology censuses were conducted approximately every ten days (* indicates monthly censusing). Sample sizes are given on the figure. The bar below the time axis indicates the drought period.

syconia on the trees in the absence of pollinators, also became extinct at this time.

In seven out of the eight species shown here the pollinators had not recolonized by October 1998, despite the availability of receptive syconia in all species from April 1998 onwards. Although small sample size precludes more detailed comment, none of the other 17 species of dioecious figs under observation bore pollinated syconia after the drought.

By contrast, in the monoecious figs (figure 2*b*), although few individuals bore syconia at the end of March 1998, wasps were immediately available when crops were initiated following the drought and hence crops were pollinated. In one species, *F. benjamina*, there were low rates of pollination amongst the first crops produced, but more than 10% of the syconia were always pollinated.

## 4. DISCUSSION

These results clearly demonstrate that in the eight species of dioecious figs at LHNP, with stable wasp populations prior to 1998, all pollinators became locally extinct during the severe drought in early 1998, and from the observations of the 17 other species it is probable that their pollinators also became extinct at this time. Furthermore, in only one out of the 25 species of dioecious figs under observation, *F. fulva*, a very common roadside species, did the pollinators recolonize before October 1998. Though in two other species, *F. schwarzii* and *F. treubii*, the pollinators had returned by April 1999, one year after the end of the drought (M. Shanahan, personal communication). Occasional observations of other dioecious figs elsewhere in Sarawak (R. D. Harrison, personal observations), Brunei (E. Jousselin, personal communication) and Sabah (Mt Kinabalu) (K. Kimura, personal communication), further suggest that pollinator extinctions were widespread, and covered most areas of Borneo affected by the drought.

Out of the 40 species of dioecious figs found at LHNP, four species are endemic to northern Borneo, while the figure for the total flora is thought to be 15 species (Corner 1965). It is quite possible that the pollinators of some of these species may be completely extinct. As fig wasps are species-specific pollinators their extinction ultimately means the extinction of the corresponding fig. The extremely high specificity of the fig–fig-pollinator interaction makes invasion by the pollinators of other fig species seem very unlikely, though it is an intriguing possibility (Kerdelhue & Rasplus 1996*a*).

When the fig pollinator is not available crops go unpollinated and consequently there is no fruit production. Yet fig fruit have often been regarded as keystone resources for vertebrate seed dispersers (Terborgh 1986; Lambert & Marshall 1991). Although detailed studies of frugivory at dioecious figs are generally lacking, fruit production in many of these figs is continuous within small groups of trees (figure 2*a*) (Corlett 1987, 1993; Harrison *et al.* 2000; R. D. Harrison, unpublished data) and this, coupled with a general paucity of other fruits in the understorey (Loiselle & Blake 1999), suggests that they are an important resource for vertebrate seed dispersers. Small fruit bats are known to be largely dependent on dioecious figs (Boon & Corlett 1989; Tan *et al.* 1998), and in LHNP evidence of feeding on *F. schwarzii* by small fruit bats was regularly found; bats were often disturbed when walking around (R. D. Harrison, personal observations). Since the drought, however, they have disappeared from this site and are scarce elsewhere in the park (M. Shanahan, personal communication). These fruit bats are important seed dispersers and ultimately there may be a knock-on effect on other tree species dependent on their services (Boon & Corlett 1989; Tan *et al.* 1998).

In an interesting contrast to the dioecious figs, monoecious fig-pollinator populations seemed little affected by the drought. Very low densities, and hence small sample sizes, and sporadic crop production make the stability of the pollinator populations before the drought difficult to assess, but syconia abortion from a lack of pollination was very rare, and immediately after the 1998 drought pollinators were available for all species that initiated crops.

Although the threshold fig population required to maintain their pollinators is particularly high in these monoecious figs, because of their intermittent fruiting, pollinators disperse long distances so populations are connected over very wide areas (Nason *et al.* 1996). When pollinators became locally extinct in Florida fig populations following Hurricane Andrew, they were available almost immediately after the initiation of new crops, as in LHNP (Bronstein & Hossaert McKey 1995). These monoecious figs were also all large hemi-epiphytes and may be pre-adapted to drought as they often suffer acute water stress during their young epiphytic phase (Holbrook & Putz 1996). This is partly supported by the fact that none of the trees lost their leaves. By contrast, dioecious figs tend to be small pioneers, in open habitats, or climbers, and are clearly prone to drought conditions. There is also some evidence that wasp dispersal is limited but that they stabilize the pollinator populations by more frequent fruiting and/or greater crop asynchrony (Corlett 1987, 1993; Kameyama *et al.* 1999).

In the dioecious figs it is possible that local extinction of pollinating wasps followed by a gradual recolonization from unaffected areas has occurred previously in Borneo, whenever there have been severe droughts. However, two worrying aspects need to be considered.

First, the 1997–1998 ENSO event and the drought it induced are the strongest yet recorded, and if the predictions of worsening and more frequent droughts (Meehl 1997; Guilderson & Schrag 1998; Timmermann *et al.* 1999) are borne out it does not bode well for dioecious figs or the organisms dependent upon them.

Second, recent forest fragmentation may also have played a role as LHNP, like most remaining forest in the region, is a small patch (6500 ha) amongst scrubby secondary forest and palm plantations. Although the densities of dioecious figs, as pioneer plants, are often very high in the secondary forest (Corner 1988; R. D. Harrison, unpublished data), the higher surface run-off and open canopy exacerbate drought conditions (Whitmore 1984). Over large areas, reduced evapotranspiration may even disrupt local climatic cycles leading to lower precipitation (Salati *et al.* 1986). For example, in Kuala Belalong, Brunei, where there are still significant areas of intact forest (>50 000 ha), the effects of drought were less severe, with monthly rainfall never dropping below 100 mm (figure 1). Significantly, in at least one species of dioecious fig at this site the pollinator wasps did not become extinct, although pollination rates were low (E. Jousselin, personal communication). Hence, it is possible that large areas of forest mitigated against droughts in the past. Furthermore, even if, as one would expect, most of these pollinator populations gradually recover from areas not affected by the drought, the impact on the vertebrate dispersers will be worsened by the small size and isolation of the remaining forest fragments.

Much of the considerable discussion about species conservation and extinction has concentrated on the viability of different population sizes (e.g. Soule & Wilcox 1980), especially of large rare species with high emotive value. However, in this case the local extinction of several extremely common species occurred when a single catastrophic event simply precluded reproduction for a period longer than the life span of an individual. Species with such brief life spans may not have so much apparent worth for conservation but if, as seen here, this also leads to the disruption of keystone interactions upon which vertebrate populations depend, then a gradual erosion of biodiversity can be expected.

I am grateful for the assistance of the Forest Research Centre, Sarawak, and for information generously provided by Emmanule Jousselin, Kazu Kimura and Mike Shanahan. Rainfall data was provided by the Malaysian Meteorological Service, Brunei Meteorological Service, Kuala Belalong Field Studies Centre and Danum Valley Field Centre. Thank you to the following and two anonymous reviewers for providing advice and comments on earlier versions of this manuscript: Dr E. A. Herre, Professor J. Lawton, Dr C. Lopez Vaamonde, Professor T. Ohgushi and Professor N. Yamamura.

## REFERENCES


Ashton, P. S. 1993 The community ecology of Asian rain forests in relation to catastrophic events. *J. Biosci.* **18**, 501–514.

Becker, P., Lye Ong, C. & Goh, F. 1998 Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica* **30**, 666–671.

Boon, P. P. & Corlett, R. T. 1989 Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). *Malayan Nat. J.* **42**, 251–256.

Bronstein, J. L. & Hossaert McKey, M. 1995 Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. *Biotropica* **27**, 373–381.

Corlett, R. T. 1987 The phenology of *Ficus fistulosa* in Singapore. *Biotropica* **19**, 122–124.

Corlett, R. T. 1993 Sexual dimorphism in the reproductive phenology of *Ficus grossularioides* Burm. f. in Singapore. *Malayan Nat. J.* **46**, 149–155.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gard. Bull. Singapore* **21**, 1–185.

Corner, E. J. H. 1988 *Wayside trees of Malaya*. Kuala Lumpur: The Malaysian Nature Society.

Galil, J. 1973 Pollination in dioecious figs: pollination of *Ficus fistulosa* by *Ceratosolen hewitti*. *Gard. Bull. Singapore* **26**, 303–311.

Guilderson, T. P. & Schrag, D. P. 1998 Abrupt shift in subsurface temperature in the tropical Pacific associated with changes in El Niño. *Science* **281**, 240–243.

Harrison, R. D. 2000 Drought and the consequences of El Niño in Borneo: a case study of figs. *Res. Popul. Ecol.* (Submitted.)

Harrison, R. D., Yamamura, N. & Inoue, T. 2000 The phenology of a common roadside fig in Sarawak. *Ecol. Res.* (In the press.)

Holbrook, N. M. & Putz, F. E. 1996 From epiphyte to tree: differences in leaf structure and leaf water relations associated with the transition in growth form in eight species of hemi-epiphytes. *Plant Cell Enviro.* **19**, 631–642.

Kameyama, T., Harrison, R. D. & Yamamura, N. 1999 Persistence of fig wasp population and evolution of dioecy in figs: a simulation study. *Res. Popul. Ecol.* **41**, 243–252.

Kerdelhue, C. & Rasplus, J. Y. 1996*a* The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure in the fig–pollinator mutualism. *Oikos* **77**, 163–166.

Kerdelhue, C. & Rasplus, J. Y. 1996*b* Non-pollinating Afrotropical fig wasps affect the fig–pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* **75**, 3–14.

Kjellberg, F., Doumesche, B. & Bronstein, J. L. 1988 Longevity of a fig wasp (*Blastophaga psenes*). *Proc. Koninklijke Nederlandse Akademie Van Wetenschappen* C **91**, 117–122.

Kudo, G. & Kitayama, K. 1999 Drought effects on the summit vegetation on Mount Kinabalu by an El Niño event in 1998. *Sabah Parks Nat. J.* **2**, 101–110.

Lambert, F. R. & Marshall, A. G. 1991 Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J. Ecol.* **79**, 793–809.

Leighton, M. & Wirawan, N. 1986 Catastrophic drought and fire in Bornean tropical rain forest associated with the 1982–83 El Niño Southern Oscillation event. In *Tropical forests and the world atmosphere* (ed. G. T. Prance), pp. 75–102. Washington, DC: American Association for the Advancement of Science.

Loiselle, B. A. & Blake, J. G. 1999 Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* **80**, 330–336.

Meehl, G. A. 1997 Pacific region climate change. *Ocean Coastal Mgmt* **37**, 137–147.

Nakagawa, M. (and 13 others) 2000 Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *J. Trop. Ecol.* (In the press.)

Nason, J. D., Herre, E. A. & Hamrick, J. L. 1996 Paternity analysis of the breeding structure of strangler fig populations: evidence for substantial long-distance wasp dispersal. *J. Biogeogr.* **23**, 501–512.

Salafsky, N. 1998 Drought in the rain forest. II. An update based on the 1994 ENSO event. *Climatic Change* **39**, 601–603.

Salati, E., Vose, P. B. & Lovejoy, T. E. 1986 Amazon rainfall, potential effects of deforestation, and plans for future research. In *Tropical forests and the world atmosphere* (ed. G. T. Prance), pp. 61–74. Washington, DC: American Association for the Advancement of Science.

SAS Institute, Inc. 1985 *SAS user's guide: basics*. Cary, NC: SAS Institute, Inc.

Soule, M. E. & Wilcox, B. A. 1980 *Conservation biology*. Sunderland, MA: Sinauer.

Tan, K. H., Zubaid, Z. & Kunz, T. H. 1998 Food habits of *Cynopterus brachyotis* (Muller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. *J. Trop. Ecol.* **14**, 299–307.

Terborgh, J. 1986 Keystone plant resources in the tropical forest. In *Conservation biology, the science of scarcity and diversity* (ed. M. E. Soule), pp. 330–344. Sunderland, MA: Sinauer.

Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. 1999 Increasing El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–696.

Tyree, M. T., Patino, S. & Becker, P. 1998 Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. *Tree Physiol.* **18**, 583–588.

Walsh, R. P. D. 1996 Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *J. Trop. Ecol.* **12**, 385–407.

Webster, P. J. & Palmer, T. N. 1997 The past and the future of El Niño. *Nature* **390**, 562–564.

West, S. A. & Herre, E. A. 1994 The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig–pollinator mutualism. *Proc. R. Soc. Lond.* B **258**, 67–72.

Whitmore, T. C. 1984 *Tropical rain forests of the Far East*, 2nd edn. Oxford University Press.

Whitmore, T. C. 1998 *An introduction to tropical rain forests*. Oxford University Press.

Woods, P. 1989 Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* **21**, 290–298.