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The impacts of large-scale, low-intensity fires on the forests of continental South-east Asia

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Abstract. South-east Asia's tropical forests harbour high levels of species richness and endemism. In continental South-east Asia strong rainfall seasonality driven by the Asian monsoon lead to ground-fires during the dry season in most years. How these fires influence the region's landscape mosaic of evergreen and deciduous forests and the biodiversity they support is poorly understood. In this paper we report on the impacts of the El Niño–Southern Oscillation-induced 1997–98 fires that burned across much of western Thailand. We compare fire effects in the three common regional forest types – seasonal evergreen (SEG); mixed deciduous (MDF); and deciduous dipterocarp – and use data from a 50-ha study plot to evaluate the impacts of fire on these forests. We found few differences among the forest types. The fires created more large gaps in MDF than the other forest types. The SEG experienced greater fire mortality in the smallest size classes, abundant resprouting, and showed some evidence of lagged mortality among larger trees. The resilience of the SEG to fire and lack of major differences in fire effects among the forest types suggest that infrequent landscape-scale fires may have little effect on biodiversity in the landscape mosaic of seasonal tropical forests of continental South-east Asia.

Introduction

In the 14th and 15th centuries, as Europeans were exploring the far reaches of their known world, map-makers would mark the end of 'discovered' lands with specific phrases to warn sailors of the uncertainty and dangers that might lie beyond. On one early representation of the known world, the Lenox Globe, a small copper sphere made in 1503, the phrase '*Hic sunt dracones*' – Here be dragons – is inscribed over the region that we now know as South-east Asia. This phrase may have originated from the legends of elemental dragons, common to many Asian cultures, that had begun to trickle back to Europe on spice-laden caravans and merchant ships. In today's world, there are few places that remain unexplored; however, 'Here be dragons' is an apt phrase to describe the current understanding of large fires in South-east Asia, for this is in many ways unexplored territory. Much of our current understanding of the role of fires in the tropical forests of South-east Asia is based on anecdote and conjecture. Few data are available on the impacts of fire in general in these ecosystems. Even less is known of large, landscape-scale fires in the region. Indeed, fundamental questions about the impacts of fires, large and small, on the structure, composition, and dynamics of tropical forests in South-east Asia remain largely unanswered and unexplored. The lack of empirical data on landscape-scale fires severely restricts the development of consistent operational guidelines and strategic policies for managing fire in the region.

The tropical forests of continental and insular South-east Asia harbor some of the highest levels of species richness and endemism in the world (Sodhi *et al*. 2004). Within the two broad biogeographic realms of the region west of Wallace's Line, the Indo-Burmese and Sundaland regions, there are hundreds of species of mammals, amphibians, and reptiles, more than a thousand species of birds, tens of thousands of plant species and untold numbers of insects. Species-level endemism varies across the different biogeographic regions of South-east Asia, but may exceed 50% across a range of phyla in some areas (e.g. Sodhi *et al*. 2004). Because of this great biological richness, both known and unknown, potential threats to tropical forests, such as unrestricted logging and hunting, fragmentation, and conversion to agriculture, represent potential threats to thousands of plant and animal species.

Forest fires are not typically considered a threat to tropical forests. However, in recent decades a growing number of studies have documented the occurrence of fires in tropical forests and their impacts on the resident flora and fauna (Sanford *et al*. 1985; Leighton and Wirawan 1986; Kinnaird and O'Brien 1998; Cochrane and Schulze 1999; Goldammer 1999; Peres 1999; Barlow *et al*. 2003*a*, 2003*b*; Cochrane 2003; Haugaasen *et al*. 2003; Slik and Eichhorn 2003). Although fires have occurred in continental and insular South-east Asia throughout the Holocene (Haberle *et al*. 2001; Penny 2001; Maxwell 2004; Hope *et al*. 2005), their geographical extent was not fully appreciated until the massive Bornean fires of 1982–83 and 1997–98. In both cases, an intense El Niño–Southern Oscillation (ENSO) event generated extreme drought conditions over continental and insular South-east Asia that were accompanied by extensive fires throughout the region. In Kalimantan alone, the fires are believed to have burned at least 5 million hectares each time, although estimates of the total area burned vary (Malingreau *et al*. 1985;

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Siegert *et al*. 2001). Such extensive fires, and the impacts they had on both human populations and biodiversity within the region, forced tropical forest scientists, policy makers, and the general public to re-evaluate their understanding of the role of fire in tropical forests and, in particular, the role of extreme climatic conditions in generating landscape-scale wildfires that could burn through even the wettest rainforests.

Although most of the attention during the 1997–98 fires was on Malaysia and Indonesia, the ENSO-induced drought led to extensive fires elsewhere in the region. Unlike the aseasonal forests of insular South-east Asia, the seasonal tropical forests on the continent experience fire relatively frequently. Each year, the Asian monsoon system generates a dry season of 2–6 months in which little to no rain falls across a region stretching from southern India to eastern Vietnam. The landscapes of this region are dominated by a patchwork mosaic of three well-described forest types – seasonal dry evergreen, mixed deciduous, and deciduous dipterocarp – that differ markedly in stand structure and species composition (Champion and Seth 1968).The seasonal evergreen forest contains the most species, has a canopy >50 m tall, and has a relatively small proportion of deciduous canopy trees, which in most years allows the relative humidity in the understorey to remain high even during the dry season. Mixed deciduous forests have fewer species, a shorter main canopy (30–40 m tall) and a majority of canopy trees that are deciduous during some or all of the dry season. The predominance of deciduous trees means that during this period considerable sunlight penetrates through to the understorey and ground layer, lowering relative humidity at ground level and increasing drying of fine fuels. Bamboos are relatively common in the mixed deciduous forest and occasional patches of grass are found throughout the forest. Many of the bamboo species of continental South-east Asia are monocarpic and flower gregariously. The synchronous mortality over large areas provides a large, but infrequent, source of fuels into the mixed deciduous forest systems and may influence local and regional fire dynamics (Keeley and Bond 1999; Saha and Howe 2001). The deciduous dipterocarp forest has the fewest tree species, being dominated by one of 5–6 deciduous dipterocarp species (e.g. *Shorea siamensis*, *Dipterocarpus obtusifolius*), the shortest main canopy (typically <25 m tall), and is almost completely deciduous for several months during the dry season. Most importantly, however, the groundstorey of the deciduous dipterocarp forest is dominated by grasses that dry during the dry season when the canopy of the forest is leafless (Troup 1921; Williams *et al*. 2008).

Although fire is a relatively common feature of continental South-east Asia, the nature of the fire regimes in the landscape mosaic of forest types is poorly understood. Because of differences in fuel composition and microclimatic conditions at the forest floor, it is widely believed that deciduous dipterocarp forests burn more frequently than mixed deciduous forests, which in turn burn more frequently than seasonal evergreen forests. Goldammer (1993) noted that deciduous dipterocarp forests may burn annually, but that the frequent, low-intensity ground-fire regime commonly associated with deciduous dipterocarp forests was likely an anthropogenic artefact. Stott *et al*. (1990) have suggested that the natural fire regime in these landscapes has a 'long-term cycle' (i.e. infrequent fires). Such assertions, however, may be misleading. First, there are no empirical data on fire histories from any forests within the region on which to base such assertions. Second, the limited anecdotal data may not be representative of current or historical fire regimes, particularly for the seasonal evergreen forests, which are often more remote and less well known. Third, the complex interdigitation of the forest types across these landscapes means that the fire regimes are likely to be highly variable spatially and temporally (as will be discussed in greater detail below).

The mosaic nature of these forested landscapes is of critical importance to the conservation of biodiversity in continental South-east Asia. Among the terrestrial fauna of tropical Asia, the larger species, especially the ungulates (e.g. elephant (*Elephas maximus*), gaur (*Bos gaurus*), banteng (*Bos javanicus*)) and carnivores (e.g. tiger (*Panthera tigris*), leopard (*Panthera panthera*)), are concentrated in these landscape mosaics of deciduous and evergreen forest. The grasses and bamboo thickets of the deciduous forests supply the main grazing during the wet season, whereas the understorey of the evergreen forest provides browse during the dry season. Importantly, the evergreen forest provides cover throughout the year. As such, maintaining an abundant and widely distributed evergreen component within the regional forest mosaic is seen as a key element of conservation plans for the terrestrial fauna of continental South-east Asia (Nakhasathien and Stewart-Cox 1990).

The occurrence of fires, therefore, raises grave concerns for regional biodiversity. Of the three dominant forest types in the region, the seasonal evergreen forest type is considered to be the most sensitive to individual fires, with most tree species believed to lack common adaptations to fire, such as thick bark or the ability to resprout vigorously (Stott 1988; Rabinowitz 1990). Studies of fire effects in Borneo in the wake of the 1998 fires have shown that fire has dramatic impacts on the community structure and composition of evergreen forests (Kinnaird and O'Brien 1998; Slik and Eichhorn 2003). Because settlement and development of formerly remote sites in continental South-east Asia have increased substantially, the forest mosaic has become increasingly fragmented in recent decades, exposing more forests to more frequent ignition sources. Conservationists are increasingly concerned that changes in fire regimes in these landscapes will reduce the area of seasonal evergreen forest and shift much of the landscape towards less evergreen forest and more deciduous forest, resulting in a net loss of species diversity as a consequence of ecosystem simplification (e.g. Ashton 1990; Rabinowitz 1990). However, this is largely unexplored territory.

Because large fires are relatively uncommon, direct observations of their impacts on forest dynamics and local species assemblages are rare, particularly for remote tropical forests. Empirical data are sorely needed to underpin the ongoing debate about fire management in the seasonal tropical forests of continental South-east Asia. In the present paper, we report on the impacts of a landscape-scale fire in deciduous and evergreen forests that occurred in western Thailand at the Huai Kha Khaeng Wildlife Sanctuary (HKK) during the 1997–98 ENSO event. Our study was an opportunistic one – such fires have only occurred three times in the past 20 years at HKK – but took advantage of a well-established research infrastructure within the sanctuary, which included a long-term forest dynamics plot that had been established 5 years before the fire. We focussed on two specific questions relevant to understanding the impacts of a large fire on the forest mosaic at HKK. First, do fire effects differ among the three major forest types found on the landscape? Second, in the more diverse, and putatively more fire-sensitive, seasonal evergreen forest, were certain species, functional groups, or size classes more prone to fire-induced mortality?

Study area

The Huai Kha Khaeng Wildlife Sanctuary is one of Thailand's premier wildlife sanctuaries and is of great conservation value. It is the second largest of 17 National Forests and Wildlife Sanctuaries that together constitute Thailand's Western Forest Complex, the largest area of contiguous protected forest in continental South-east Asia. The forests in the Western Forest Complex support a wide range of threatened and endangered plant and animal species including tigers, clouded leopards, elephants, banteng and gaur (Nakhasathien and Stewart-Cox 1990). In recognition of their importance for the conservation of the regional flora and fauna, HKK and the neighbouring Thung Yai-Naresuan Wildlife Sanctuary were awarded UNESCO World Heritage Site status in 1991.

Fires are a recurrent event at HKK. In the past two decades, fires have been recorded somewhere within the sanctuary nearly every year, although sanctuary-wide fires occur much less frequently (1991, 1998, 2004). Increasing population densities and agricultural activities adjacent to the buffer zone surrounding HKK have led to a ready ignition source. Although extensive landscape-scale fires are relatively rare, there is concern that incursions of fire into the species-rich seasonal evergreen forests are becoming more common and pose a serious threat to its long-term presence across the landscape (Rabinowitz 1990). The 1998 fires, which burned through $\sim$1500 km^2 of forest, were the largest fires at HKK in at least the past 30 years.

Since 1991, forest scientists from the Royal Forest Department of Thailand, the National Parks, Wildlife and Plant Conservation Department, and the Center for Tropical Forest Science of the Smithsonian Institution have been working together on the establishment and maintenance of a large-scale, permanent forest dynamics study plot in seasonal evergreen forest at HKK. The plot, which covers 50 ha and includes every tree $>$1 cm diameter at breast height (DBH), includes 80 000 trees from 291 species and has been measured three times (in 1994, 1999, and 2004). In February and March of 1998, the HKK fires burned through the 50-ha plot and adjacent areas of mixed deciduous and deciduous dipterocarp forest, providing a unique opportunity to describe and compare the impacts of a landscape-scale fire on each of the major forest types and to examine the potential role of large fires in structuring and maintaining the landscape forest mosaic.

Methods

Fire intensity and fire-induced mortality among forest types

To determine if landscape-scale fires have different impacts on the different forest types, we conducted an intensive survey of tree mortality, as well as an extensive survey of fire-induced gap formation in each of the three forest types. For our intensive survey of fire effects in each forest type, we established two 20×125 m transects $<$1 week after fire (March 1998) in areas of seasonal evergreen, mixed deciduous and deciduous dipterocarp forest that had been burnt by the fires. Each transect was divided into 100 5×5 m quadrats. To characterise the relative intensity of the fire within each quadrat, we recorded whether fire had occurred in each quadrat, the percentage of the quadrat area that had been burned, and the average crown scorch height within the quadrat based on loss or scorching of leaves. Within each transect, we also used a nested sampling design to characterise tree abundance and mortality in different size classes. We identified and measured all trees ($>$10 cm DBH) within 10 m of the transect, all poles (4.5–10 cm DBH) within 5 m of the transect, and all saplings (1–4.5 cm DBH) within 1 m of the transect. The total sample area for each transect was 2500 m^2, 1250 m^2, and 250 m^2 for trees, poles, and saplings, respectively. In addition, we tallied, but did not identify, seedlings ($<$1 cm DBH) in 1-m^2 plots every 5 m along the transect. The total sample area for seedlings in each transect was 25 m^2. For all trees, poles, and saplings, the following information was recorded at the time the transect was established: species, DBH, crown scorch, and whether the individual was dead or alive. Crown scorch was scored from 1 to 5 (1 = 80–100%, 2 = 60–80%, 3 = 40–60%, 4 = 20–40%, and 5 $<$20% crown scorch); deciduous species were noted. Each transect was revisited at the end of the rainy season (November 1998, $\sim$8 months after fire) and the following information was recorded for each individual: dead or alive, presence or absence of sprouting, and the presence or absence of basal scarring.

To characterise the stand-scale impacts of the fires, we estimated the number and size of canopy gaps that were created by fire-killed trees in each forest type. For the seasonal evergreen forest, a detailed assessment of damage was conducted in the 50-ha plot. Using the 20×20 m grid system within the plot, 26 parallel 1000-m transects were established, beginning from the northern edge of the plot. The size of each canopy gap created by a fallen tree or group of trees was measured in two perpendicular directions and calculated as the area of an ellipse. The mode of death for each fallen tree was recorded as burnt-out above or below 2 m height on the stem, or as incidental mortality (knocked over by a falling tree). Large permanent study plots were not available for the mixed deciduous and deciduous dipterocarp forests types. Instead, within each forest type, we selected a large area of relatively homogeneous forest where we established series of parallel transects $\sim$30 m apart and of varying length. All fire-killed trees $>$10 cm DBH that had fallen within 15 m of the transect were identified and measured. Total areas sampled for the mixed deciduous and deciduous dipterocarp forests were 12.5 and 12.1 ha, respectively. All three forest types were sampled 4–6 weeks after the fires had occurred. The total area of canopy gaps created by the fires and the size distribution of the canopy gaps were calculated for each forest type. We compared gap size distributions among forest types using non-parametric Kruskal–Wallis ANOVA.

Fire-induced mortality in the seasonal evergreen forest

To assess whether specific elements of the seasonal evergreen forest community are particularly susceptible to fire, we used the 50-ha plot database to compare species-specific mortality and abundance patterns for seasonal evergreen forest tree species during 1994–99, the period in which the 1998 fires occurred, and 1999–2004, when no fires entered the plot. The 1999 census was initiated in May 1998, 2 months after the fires occurred, and completed ∼10 months later. We fitted locally weighted smoothing (Loess) splines and estimated confidence intervals for mortality as a function of tree size (DBH) for each species separately and for all species pooled for the fire interval and the non-fire interval. The Loess smoothing splines are fitted to a variable probability sample of size 4000 from the measured trees of each species, selected with probability proportional to tree size. If there were fewer than 4000 representatives from the species, then all trees were used. We used a sample size of 4000 to work around memory limits of the available algorithms. The Loess fitting algorithm used the sampling weights, if sampling was done. We also examined whether tree species from different functional groups (evergreen *v.* deciduous) or possessing certain life-history traits (large size: 90th percentile DBH; fast growth: 90th percentile growth rate) were more or less prone to fire-induced mortality. To determine whether tree species in the seasonal evergreen forest were capable of sprouting, we checked the 50-ha plot database for records of basal sprouts from trees in the post-fire census period.

Results

Comparison of fire effects across the three forest types revealed few differences. Nearly every study quadrat in each forest type was burned. The proportion of each quadrat burned ranged from 20 to 100%, but did not differ significantly among forest types. Mortality patterns were heterogeneous among size classes and forest types. The greatest difference was between sapling mortality in seasonal evergreen forest (24%) and mixed deciduous forest (63%); however, most of the mixed deciduous forest species resprouted several months after the fire. Basal scarring was greater in the seasonal evergreen forest (55%) than in the mixed deciduous (32%) and deciduous dipterocarp forests (30%). Scorch heights ranged from 0 m in unburned quadrats to 4 m in a single quadrat in the seasonal dry evergreen forest. The distribution of scorch heights did not differ significantly among forest types, although the mixed deciduous forest had a slightly lower mean scorch height (1.12 ± 0.53 m) than the seasonal evergreen (1.46 ± 0.67 m) and deciduous dipterocarp (1.48 ± 0.48 m) forests (Fig. 1).

In contrast, the stand-scale assessment of fire impacts on canopy gap formation revealed substantial differences among forest types. In the deciduous dipterocarp and seasonal dry evergreen forest types, there was relatively little canopy disturbance. In contrast, the mixed deciduous forest suffered substantial canopy disturbance from the fire. Canopy gaps ranging from 25 to 1000 m^2 were created in the three forest types during the fires and for ∼2 months afterward. In the 50-ha plot, the 1998 forest fires created 85 new gaps, or 1.7 gaps ha^{-1} and mean gap size was ∼95 m^2 (Fig. 2). The total area of fire-created gaps in the seasonal evergreen forest was 1.61% of the total area surveyed. In the 12.5 ha of deciduous dipterocarp forest, only three small (mean gap size = 35 m^2) gaps occurred as a result of the fires. The few fire-induced canopy gaps and their small size accounted for only 0.09% of the deciduous dipterocarp forest canopy being disturbed by the 1998 fires at HKK. In the 12.1-ha study area of mixed deciduous forest 5 km to the east of the 50-ha plot, the fires created 52 gaps (4.3 ha^{-1}) with a mean gap size of 105 m^2.

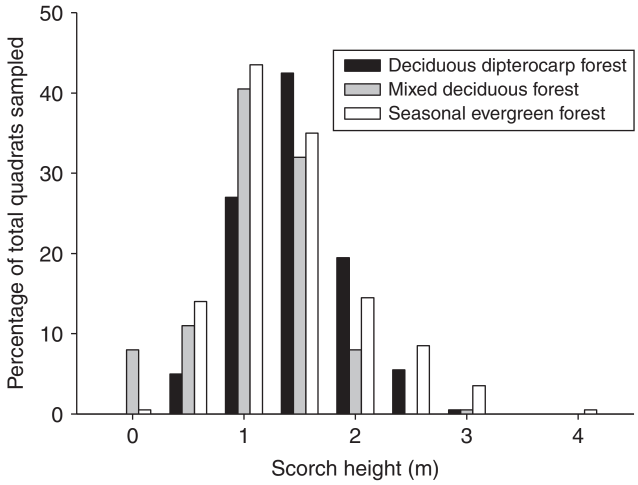

Fig. 1. Distribution of scorch heights among the three forest types: seasonal evergreen forest (SEG), mixed deciduous forest (MDF), and deciduous dipterocarp forest (DDF). In each forest type, scorch height was measured in 100 contiguous quadrats within each of two transects. Scorch height was determined based on the average height of leaf and crown scorch within each quadrat.

Although the mixed deciduous forest gaps were slightly larger than those in the seasonal dry evergreen forest, the greater frequency of gaps in the mixed deciduous forest meant that the total area of fire-created gaps (4.5%) was substantially greater than in the other two forest types.

Within the species-rich seasonal evergreen forest, detailed analysis of demographic data from the 50-ha plot revealed several striking patterns. First, there were significant differences in mortality patterns between the first (fire) and second (fire-free) census intervals (Fig. 3). Overall mortality was higher in the first interval (6.7%) than the second interval (4.2%). There were also distinct patterns in size-dependent mortality. Mortality rates among small trees (<2 cm DBH) were nearly twice as great in the first census (Fig. 3) owing to their shorter stature (and consequently greater crown scorch) and thinner bark (Baker and Bunyavejchewin 2006). Mortality rates during the fire interval (i.e. intercensus period 1994–99 during which the 1998 fire occurred) were also higher for trees 20–40-cm DBH, but were not substantially different for trees >40 cm DBH. Examination of mortality profiles for several abundant species demonstrated that the plot-wide patterns masked considerable interspecific heterogeneity in fire-induced mortality (Fig. 4). In most cases, the smallest trees experienced higher mortality rates during the fire interval than the non-fire interval – the two dominant dipterocarps of the forest canopy, *Hopea odorata* and *Dipterocarpus alatus*, being the exceptions. An interesting feature of the species-specific comparisons of mortality rates is that during the fire-free interval, several species had higher mortality rates in the largest size classes. Species exhibiting this pattern were all large canopy species and included *Hopea odorata*, *Dipterocarpus alatus*, *Neolitsea obtusifolia*, *Tetrameles nudiflora*, and *Saccopetalum lineatum*. Observations in the years following the fires suggest that among large trees, fire-induced mortality may be subject to temporal lags as the fire-scarred bases or weakened

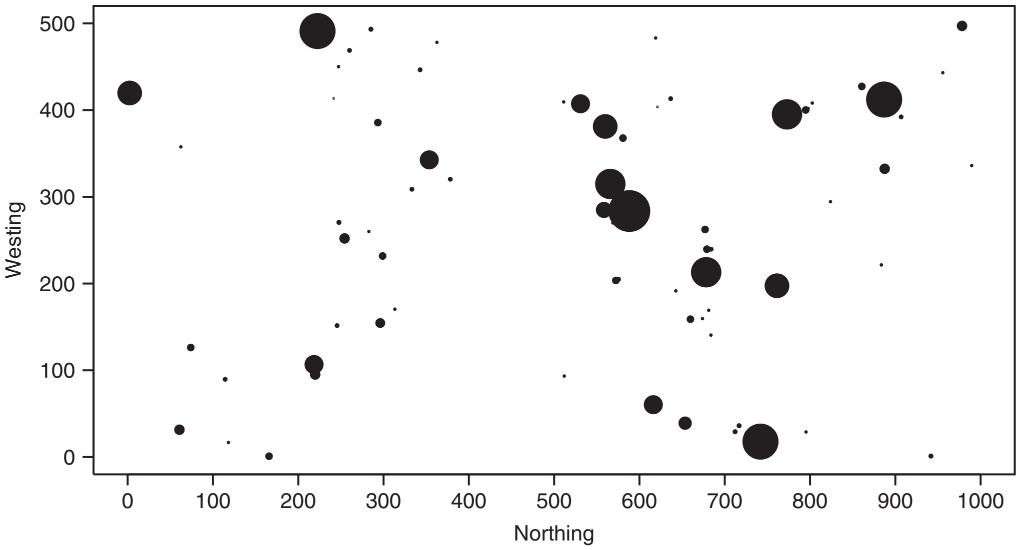

Fig. 2. Location of all 85 gap-creating treefalls created by the 1998 El Niño–Southern Oscillation (ENSO)-associated fires as they burned through the Huai Kha Khaeng 50-ha plot.

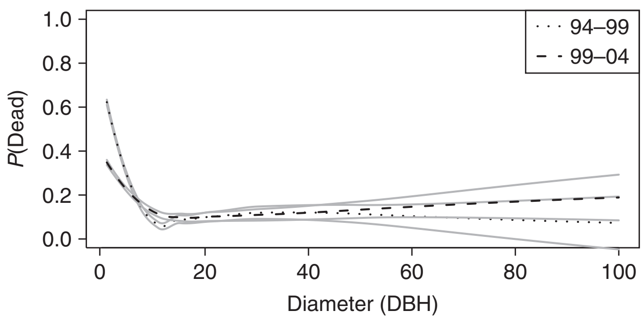

Fig. 3. Loess-smoothed estimates of the probability (*P*) of mortality rates for the two intercensus intervals (1994–99 and 1999–2004) as a function of diameter at breast height (DBH, cm) for all trees on the Huai Kha Khaeng 50-ha plot. The grey lines around each smoothing represent one standard error in each direction.

buttress roots increase a tree's susceptibility to being toppled by wind storms associated with the onset of the annual summer monsoon. Haugaasen *et al*. (2003) have reported similar lagged mortality among large trees subject to low-intensity ground fires in the Amazon. The only other large canopy tree, *Vatica odorata*, showed no difference in large tree mortality during the fire- and fire-free intervals. In contrast, the mid-storey trees *Baccaurea ramiflora*, *Croton roxburghii*, and *Polyalthia viridis* all had greater mortality in the large size classes during the fire interval.

Multiple censuses for such a large number of trees and species at the HKK 50-ha plot also allowed us to determine the effects of the fire on species loss and species immigration. Our data show that neither species richness nor abundance was substantially affected by the fire. Most species changed relatively little in abundance (Fig. 5). Nine species were lost and four species gained between the 1994 and 2004 censuses. All of the species that were lost between 1994 and 2004 were rare – none had >40 individuals in 1994. However, among individual species, the fire produced some clear winners and losers. *Croton roxburghii*, the most abundant species on the plot, increased in abundance by 250% (11 411 stems to 28 778 stems). In contrast, *Solanum erianthum*, an understorey treelet, lost most of its population (1504 stems to 14 stems). The 50-ha plot data also demonstrate that many of the species in the seasonal evergreen forest do resprout after fires. During the 1999 recensus, which was conducted in the months that followed the 1998 fire, we recorded for every stem whether basal sprouts were present. We recorded sprouting in 163 species from the 50-ha plot. Although sprouting occurred in trees ranging from 1 to 50 cm DBH, sprouting was much more common and prolific in the smallest stems. In some instances, as many as 25 sprouts were recorded on a single tree; the median number of sprouts per tree was two (Fig. 6).

Comparison of functional groups and life-history traits revealed little evidence of differential mortality as a consequence of the fire. Pre- and post-fire abundances were similar for deciduous and evergreen species (Fig. 5). Fire-associated mortality was correlated with tree stature, measured as the 90th percentile DBH of each tree species, but not with growth rate, measured as the 90th percentile DBH growth rate of the species (Fig. 7). The relationship between mortality and tree stature was strongly negative between 1 and 15 cm, after which there was little change in the probability of mortality with increasing stature.

Discussion

Landscape-scale fires in continental and insular South-east Asia are widely believed to be detrimental to biodiversity within the region (e.g. Rabinowitz 1990; Taylor *et al*. 1999; Sodhi *et al*. 2004). Short-term studies and anecdotal observations suggest that wildlife is impacted directly through fire-induced mortality (e.g. Stott 1986; Kinnaird and O'Brien 1998) or indirectly as forest trees, which provide habitat and serve as food sources, are

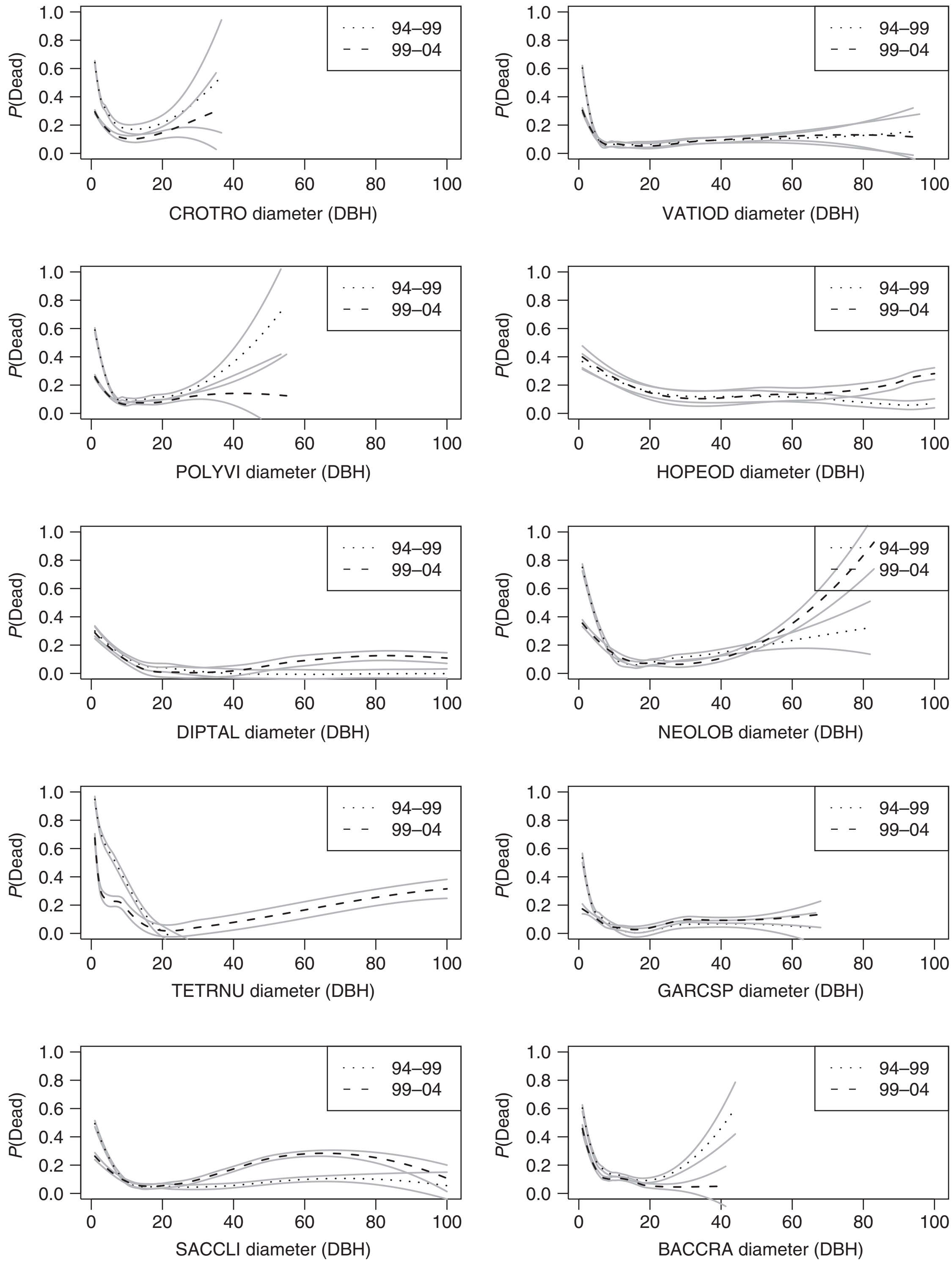

Fig. 4. Loess-smoothed estimates of the probability (*P*) of mortality rates as a function of diameter at breast height (DBH, cm) for 10 common species on the Huai Kha Khaeng 50-ha plot. Species abbreviations are *Baccaurea ramiflora* (BACCRA), *Croton roxburghii* (CROTRO), *Dipterocarpus alatus* (DIPTAL), *Garcinia speciosa* (GARCSP), *Hopea odorata* (HOPEOD), *Neolitsea obtusifolia* (NEOLOB), *Polyalthia viridis* (POLYVI), *Saccopetalum lineatum* (SACCLI), *Tetrameles nudiflora* (TETRNU), and *Vatica odorata* (VATIOD). The grey lines around each smoothing represent one standard error in each direction.

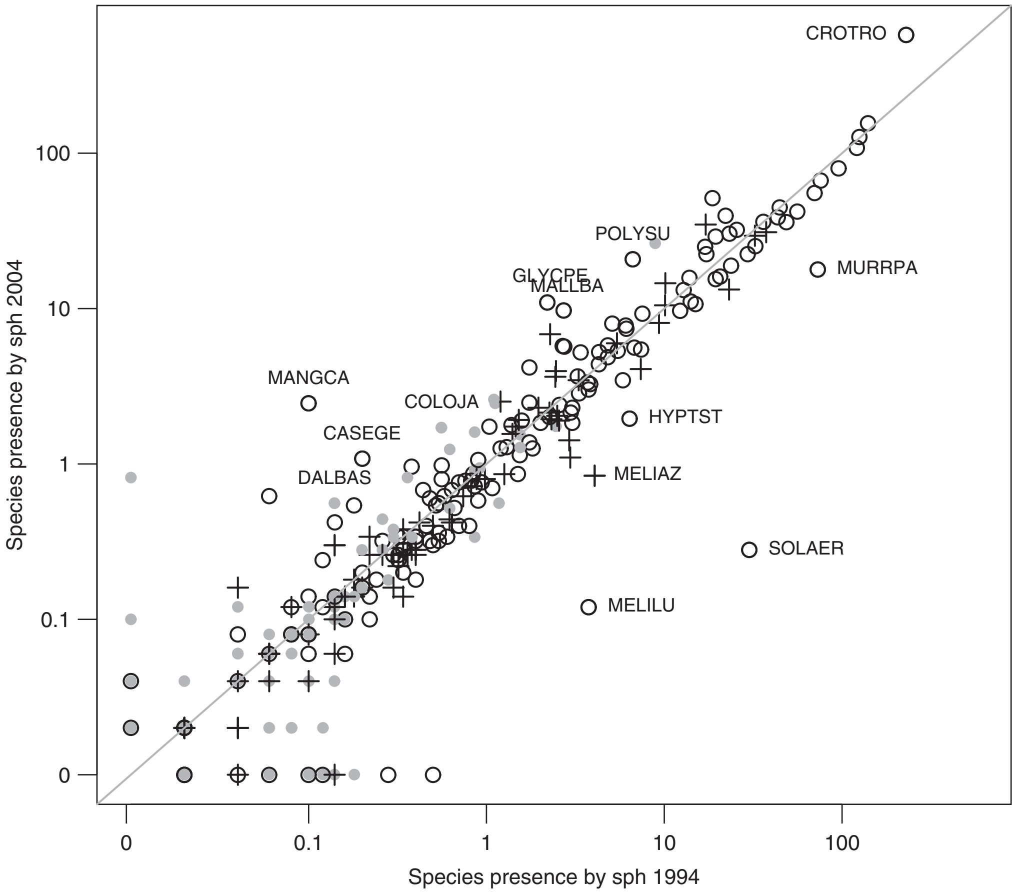

Fig. 5. Comparisons of species-specific abundances between the first census interval, during which the 1998 fires occurred, and the second census interval, which was fire-free. Values are in stems per hectare (sph). Evergreen species are denoted with an empty circle and deciduous species with a cross. For some species, mostly those of low abundance, the phenology is not known; these species are represented by a full grey circle. A line depicting a 1 : 1 relationship is drawn as a guide. Species that did not change in abundance between census intervals are located on the line. Species that increased in abundance are above the line; species that decreased in abundance are below the line. Species that were lost from the plot after the fire are on $y = 0$; species that appeared in the plot following the fire are on $x = 0$. The species identified in the graph are those with the greatest difference in population density between intercensus intervals. Species abbreviations are *Casearia grewiifolia* (CASEGE), *Croton roxburghii* (CROTRO), *Colona javanica* (COLOJA), *Dalbergia assamica* (DALBAS), *Glycosmis pentaphylla* (GLYCPE), *Hyptianthera stricta* (HYPTST), *Mallotus barbatus* (MALLBA), *Mangifera caloneura* (MANGCA), *Melia azederach* (MELIAZ), *Melicope lunaankenda* (MELILU), *Murraya paniculata* (MURRPA), *Polyalthia suberosa* (POLYSU), *Solanum erianthum* (SOLAER).

killed by the fires (e.g. Rabinowitz 1990; Kinnaird and O'Brien 1998). However, empirical evidence of catastrophic impacts by fire in South-east Asian forests and their associated flora and fauna is limited. This may be because there are few studies that have documented the long-term impacts of fire on these forests or, alternatively, the fires have less impact than previously believed.

The HKK Wildlife Sanctuary is one of the few sites in continental South-east Asia where research on the impacts of landscape-scale fires have been conducted in an area within which the forests are very well studied. The ENSO of 1997–98 generated extremely dry conditions at HKK that allowed several small fires on the periphery of the sanctuary in January 1998 to become a much larger landscape-scale fire front that over the next 3 months burned hundreds of square kilometres of forest. The status of HKK in Thailand as a national conservation icon meant that the 1998 fires were heavily covered in the national media – on several occasions appearing on the front page of every national newspaper simultaneously. Inevitably, the media reported the fires as ecological catastrophes (e.g. 'When Nature Goes on a Fiery Rampage', *Bangkok Post*, 18 February 1998). Our study of fire impacts across the landscape mosaic of forest types at HKK suggested that the impacts of these fires on the abundance and composition of tree species were relatively limited, even in the putatively fire-sensitive seasonal evergreen forest. We had anticipated that the substantial differences in forest structure and composition among the three major forest types at HKK would lead to large differences in the amount of damage

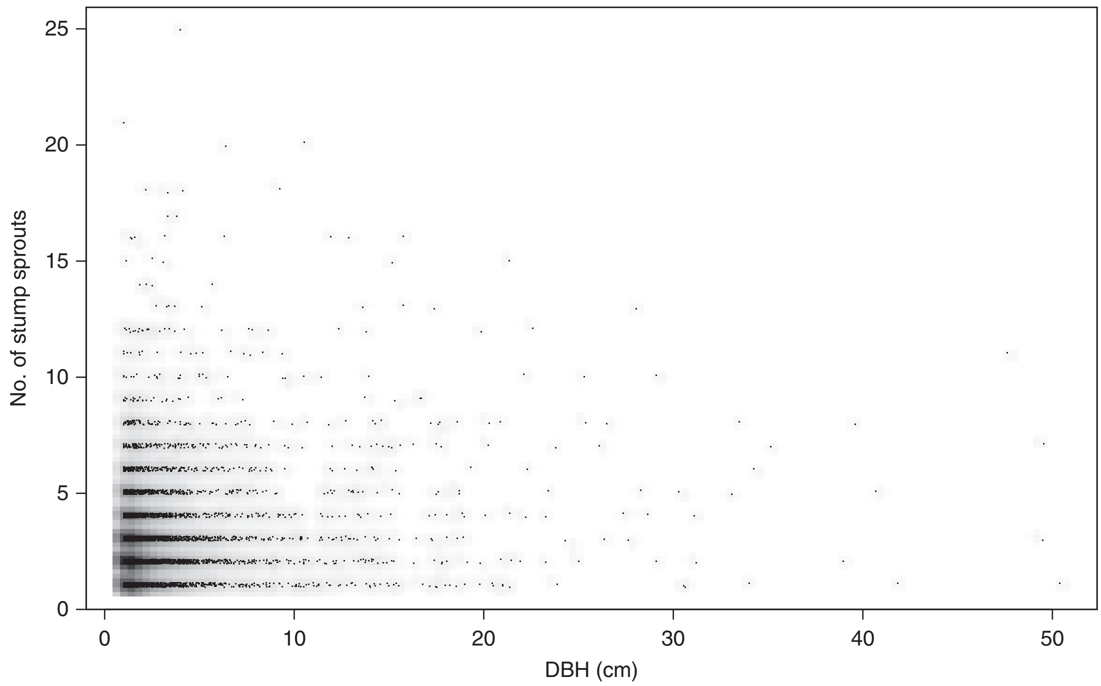

Fig. 6. Relationship between number of basal sprouts on a tree stem and the diameter at breast height (DBH) of the tree. Owing to the large number of tree stems with sprouts ($n = 8504$) in the 50-ha plot database, individual points have been jittered by 20% and overlain on a bivariate density plot to illustrate the relative abundance of number of stems as a function of DBH.

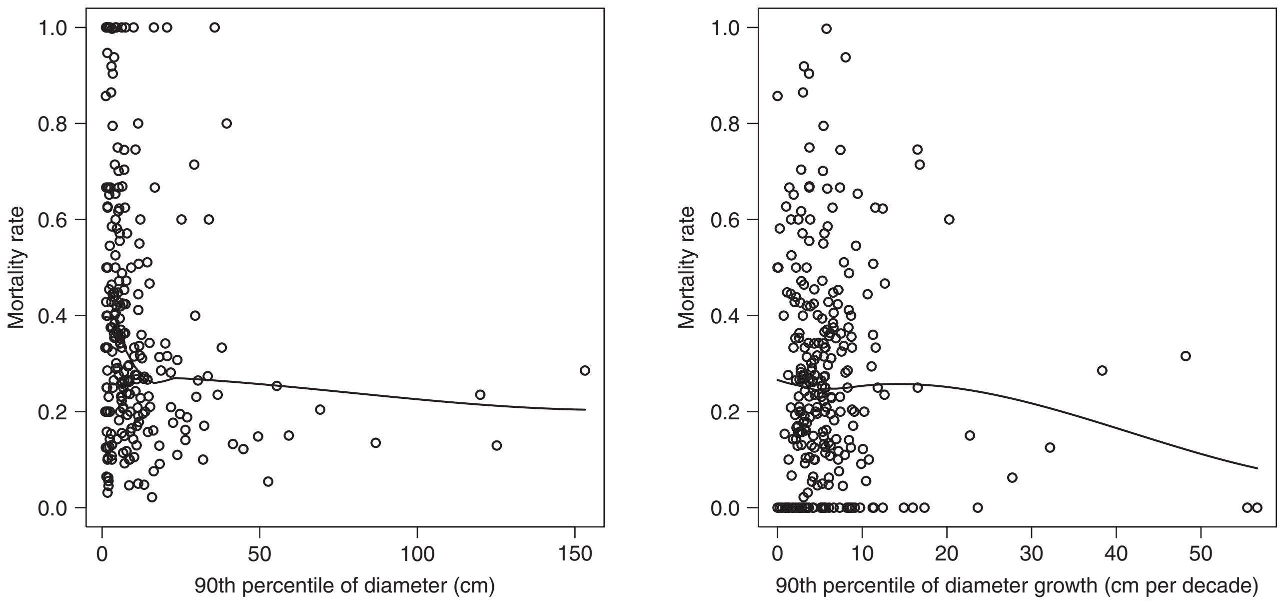

Fig. 7. Probability of mortality as a function of two life history traits: tree stature (left panel) and tree growth rate (right panel). Each point represents one species and is based on the 90th percentile diameter at breast height (DBH) (left panel) or 90th percentile DBH growth rate (right panel) calculated from the 50-ha plot data. A Loess smoothing spline indicates the locally weighted mean values as a function of either tree stature or tree growth rate.

that they incurred in the fires. Instead, we found that among the forest types, there were relatively few differences in fire extent, relative fire intensity (estimated from scorch height), and mortality patterns across a range of size classes.

Despite the wide areal extent of the fires and the extreme climatic conditions, the fires were predominantly low-intensity surface fires with flame lengths ranging from 5 to 50 cm. The fires never entered the canopy in any of the forest types and, in general, appeared to affect only trees <2 m tall. Other studies have shown that fires in tropical forests are often low-intensity surface fires and that the initial impact of the fire is to kill the aboveground portions of the smallest trees (e.g. Cochrane and Schulze 1999; Peres 1999). One reason that fire impacts may vary little among forest types is that fire intensity is consistently low in each forest type. Despite differences in fine fuel composition on the forest floor, scorch heights were not different among the forest types. This is most likely a consequence of the interaction between flame length and the speed of the fire front (Agee 1993). In the deciduous dipterocarp forest, the groundstorey vegetation is dominated by grasses and herbaceous vegetation. Flame lengths in these areas can be relatively high (50–150 cm), but the open understorey allows the fire to progress quickly through the stand. In contrast, the seasonal evergreen forest understorey is dominated by tree seedlings and leaf litter. Flame lengths are shorter (5–30 cm), but the fire moves much more slowly through the forest.

Within the seasonal evergreen forest, the 1998 fire led to widespread aboveground mortality, despite the fire intensity being relatively low. Low-intensity surface fires are typical in tropical forests, particularly those in less seasonal environments or in relatively moist edaphic conditions (e.g. Cochrane and Schulze 1999; Peres 1999). Although the impacts of these fires on wildlife may be limited, as many can move out of the way of the slowly advancing fireline, the fires may influence community composition. Kinnaird and O'Brien (1998) noted that species richness and abundance of the bird community in the wake of the 1998 fires in evergreen forests in Sumatra did not change. However, they found that the mortality of canopy trees led to a decrease in frugivores and an increase in insectivores, such as woodpeckers, which feed on wood-boring beetles that attack injured or recently killed trees. What the long-term consequences of the 1998 fires will be on bird communities or other species assemblages at HKK is unknown. Long-term studies that document changes in community composition of the flora and fauna in the wake of landscape-scale fires are sorely needed across the region.

We found that in the immediate aftermath of the 1998 fire, most mortality was in the smallest size classes (<5 cm DBH). Not surprisingly, the stature of a species as measured by its 90th percentile DBH was strongly correlated with its susceptibility to fire-induced mortality. This suggests that those small-statured tree species that lack adaptations to fire, such as resprouting or a persistent soil seedbank, will be most sensitive to changes in population size induced by large fires. In contrast, small-statured species that are well adapted to fire, such as *Polyalthia suberosa*, which has particularly thick, corky bark, may benefit from the fires (Fig. 5). Many studies in both temperate and tropical regions have demonstrated that fire-induced mortality is often size-dependent for trees because larger trees have thicker bark and are better able to protect the vascular cambium from catastrophic heating (e.g. Gill and Ashton 1968; Hengst and Dawson 1994; Pinard and Huffman 1997). Slik and Eichhorn (2003) also found similar patterns of size-dependent mortality among evergreen rainforest trees in East Kalimantan following the 1998 fires. Mortality was not restricted to the smallest trees, however. We found evidence of a distinct delay in fire-induced mortality among large trees of several abundant canopy tree species. Haugaasen *et al*. (2003) found a similar pattern of delayed mortality in large trees after low-intensity surface fires in tropical forest in the Central Amazon.

The size-dependent patterns of aboveground mortality and dieback are counterbalanced by size-dependent patterns of resprouting. Smaller trees were more susceptible to fire-induced mortality, but were also more likely to resprout, often vigorously, within months of the fire. For the seasonal evergreen forest, which has long been considered the most sensitive of the main forest types to fire, the outcome of these opposing dynamics is a forest little changed by the 1998 ENSO fires. We found little impact of the fires on community composition and population size structures within the seasonal evergreen forest. A recent study has shown that there is no relationship between bark thickness, a common surrogate for heat resistance (and therefore fire tolerance), and various measures of population size structures for 10 of the dominant tree species on the 50-ha plot (Baker and Bunyavejchewin 2006).Our results are in direct contrast to those from the aseasonal forests of South-east Asia that experienced significant changes in structure and composition after the 1998 fires (e.g. Slik and Eichhorn 2003; Cleary *et al*. 2006). Although the lack of long-term studies of forest composition change following large, landscape-scale fires limits our ability to generalise our results, which derive from a single extreme fire event from a single landscape within continental South-east Asia, they do suggest that the ability to withstand individual fire events may be a fundamental character that distinguishes the lowland evergreen dipterocarp forests of seasonal South-east Asian environments, located primarily in continental sites, from their aseasonal analogues across the region (Baker and Bunyavejchewin, in press).

In continental South-east Asia, there is concern that an increase in fire frequency would allow the less diverse deciduous dipterocarp or mixed deciduous forest types to invade and gradually replace the more species-rich seasonal evergreen forest (Stott 1988; Rabinowitz 1990). Previous studies at HKK have shown that seedlings of common tree species from the seasonal evergreen and mixed deciduous forests grow equally well when planted in gaps in either forest type (Baker 1997). In a follow-up survey 10 years after the seedlings were planted, we found that the only species to survive in the fire-prone mixed deciduous forest was *Hopea odorata*, the dominant canopy tree species in the seasonal evergreen forest, despite having been exposed to three fires in a decade. More extensive studies of how tree species from each of the forest types regenerate and how fires impact this regeneration are needed before it is possible to assess potential shifts in the relative abundance of the evergreen and deciduous forest types.

An overarching theme of the present review has been the lack of data on the impacts of large-scale fires on biodiversity in South-east Asia. Detailed data on tree species mortality and abundance from the HKK 50-ha plot and surrounding stands of mixed deciduous and deciduous dipterocarp forests in the wake of the 1998 ENSO-associated fires provide much needed empirical data on the impacts of landscape-scale fires in the seasonal forests of mainland South-east Asia. Although the results suggest that landscape-scale fires in the forest mosaic of continental South-east Asia may not be particularly disastrous for tree species, there remain many unanswered questions. For example, can the effects of a single, landscape-scale fire burning at low intensity have long-term consequences for variability in demography? Can variability in demography, combined with widespread heterogeneity in local fire intensity and canopy gap formation, provide a mechanism for the tree species and forest types to coexist in mosaic fashion across the landscape? Despite our concerns for the remarkable diversity associated with the tropical forests of South-east Asia, we will not make progress in understanding how landscape-scale fires influence the structure and composition of the forest and the distribution and abundance of its inhabitants across a range of spatial and temporal scales without substantial increases in fire ecology research in South-east Asia. *Hic sunt dracones*.

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