Austral Ecology (2008) **33**, 399–408

Impacts of wind disturbance on fragmented tropical forests: A review and synthesis

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Abstract Wind disturbance is an important ecological force in the tropics, especially in the cyclonic and hurricane zones from about 7–20° latitude. Damage from intense winds may be especially severe in fragmented forests because of their abrupt artificial margins and denuded surrounding landscapes. We review available information on the effects of windstorms on fragmented forests, synthesizing studies from Australasia, Amazonia and elsewhere in the tropics. Wind damage in fragmented landscapes can be influenced by a range of factors, such as forest-edge orientation, edge structure, the size of nearby clearings and local topography. We argue that wind disturbances are likely to interact with, and exacerbate, a range of deleterious environmental changes in fragmented forests. Among the most important of these are altered forest structure, shifts in plant species composition, exotic-plant invasions, reduced carbon storage and elevated vulnerability to fire. The damaging impacts of winds on fragmented forests could potentially increase in the future, particularly if global warming leads to increasingly severe or frequent windstorms.

Key words: edge effect, forest dynamics, habitat fragmentation, plant functional trait, windstorm resistance and resilience.

INTRODUCTION

Intense winds can seriously damage tropical forests (Whitmore 1974; Everham & Brokaw 1996). Here we assert that wind disturbance can be exceptionally severe in fragmented tropical forests, and suggest that this could have important implications for forest conservation.

Our argument is based on four observations. Firstly, wind disturbance is a potent ecological force across much of the tropics, especially in the cyclonic and hurricane zones from about 7–20° latitude (Webb 1958; Lugo *et al.* 1983; Bellingham *et al.* 1996; Lugo 2008), but also in equatorial forests affected by convectional thunderstorms (Nelson *et al.* 1994) and strong prevailing winds (Laurance 1997).

Secondly, as detailed below, fragmented forests are thought to be inherently vulnerable to wind damage. Such disturbances, although incompletely understood, can alter many aspects of forest ecology, including vegetation structure, species composition, carbon storage and ecosystem functioning (Boose *et al.* 1994; Everham & Brokaw 1996; Laurance 1997; Laurance *et al.* 1997, 1998a, 2006a; Curran *et al.* submitted).

Thirdly, the total area of tropical forest that is fragmented is increasing rapidly. Over the last quarter century, global rates of tropical deforestation have averaged 10–15 million hectares annually (FAO 2001; Achard *et al.* 2002) – or roughly 40–60 football fields per minute – the aftermath of which includes vast expanses of fragmented forest. Moreover, such figures fail to include many forms of forest degradation, such as industrial logging, surface fires, overhunting and edge effects, which can also have serious impacts on forest ecosystems (Asner *et al.* 2006; Laurance & Peres 2006).

Finally, some evidence suggests that the frequency of megastorms (those rated at Categories 4 and 5, using the Saffir-Simpson scale) could rise in the future as a result of global warming (Hughes 2003; Mann & Emanuel 2006; but see Turton 2008). Cyclones and hurricanes are, fundamentally, giant engines for dispersing heat from the tropical ocean surface. As global temperatures rise, so will ocean-surface temperatures, and thus the intensity and destructiveness of storms could increase as well. Recent modelling studies suggest that rising global temperatures may have little impact on storm frequency, but strong effects on storm severity (Walsh & Ryan 2000; Emanuel 2005). These modelling studies are bolstered by an observed increase in severe-storm frequency in recent decades

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doi:10.1111/j.1442-9993.2008.01895.x

(Goldenberg *et al.* 2001; Webster *et al.* 2005; but see Nyberg *et al.* 2007).

Here we synthesize available research on known and potential impacts of windstorms on fragmented tropical forests (see Everham & Brokaw 1996) for a general review of wind effects on forests). We show that winds can have serious impacts on fragmented forests, altering many aspects of forest dynamics and functioning, and we highlight fragment- and landscape-scale factors that can influence wind disturbance. We then argue that wind disturbance is likely to exacerbate some the most deleterious effects of habitat fragmentation.

WIND AND FRAGMENTED FORESTS

Fragmented forests appear to be particularly vulnerable to wind disturbance, for two reasons. First, denuded lands surrounding forest fragments provide less resistance to winds than do forests, allowing wind speeds to accelerate across the cleared landscape (Savill 1983). Second, forest fragmentation leads to a drastic increase in the amount of abrupt, artificial forest edge (Fig. 1), which is inherently susceptible to wind disturbance.

As a result of these changes, forest remnants are exposed to increased wind speed, turbulence and vorticity (Bergen 1985; Miller *et al.* 1991). Winds striking an abrupt forest edge can exert strong lateral-shear forces on exposed trees and create considerable downwind turbulence for at least 2–10 times the height of the forest edge (Somerville 1980; Savill 1983). Greater wind speeds increase the persistence and frequency of wind eddies near edges that can heavily buffet the upper 40% of the forest (Bull & Reynolds 1968). In concert with increased desiccation and other microclimatic stresses near edges (Kapos 1989; Turton & Freiberger 1997), wind disturbance has been shown in some cases to cause sharply elevated tree mortality inside forests within approximately 100–500 m of forest edges (Fig. 2; Laurance 1991; Laurance *et al.* 1998a; D'Angelo *et al.* 2004; but see Pohlman *et al.* 2008). Large (>60 cm diameter) trees in fragments appear especially vulnerable (Laurance *et al.* 2000).

Elevated tree mortality has myriad impacts on fragmented forests. It fundamentally alters canopy-gap dynamics (Young & Hubbell 1991; Laurance *et al.* 1998a; Lewis 1998), which in turn influences forest structure, composition and diversity. Smaller fragments often become hyper-disturbed, leading to surprisingly rapid changes in floristic composition (Laurance *et al.* 2006a). New trees regenerating near forest edges are significantly biased towards disturbance-loving pioneer and secondary species and against old-growth, forest-interior species (Viana *et al.* 1997; Laurance *et al.* 1998b, 2006a, 2006b). Lianas – important structural parasites that reduce tree growth, survival and reproduction – increase in density near edges and may further elevate tree mortality (Oliveira-Filho *et al.* 1997; Viana *et al.* 1997; Laurance *et al.* 2001). Leaf litter accumulates near edges (Sizer *et al.* 2000; Vasconcelos & Luizão 2004) as drought-stressed trees shed leaves, and may negatively affect seed germination (Bruna 1999) and seedling survival (Scariot 2001; Sanchez-Thorin *et al.* 2006). Finally,

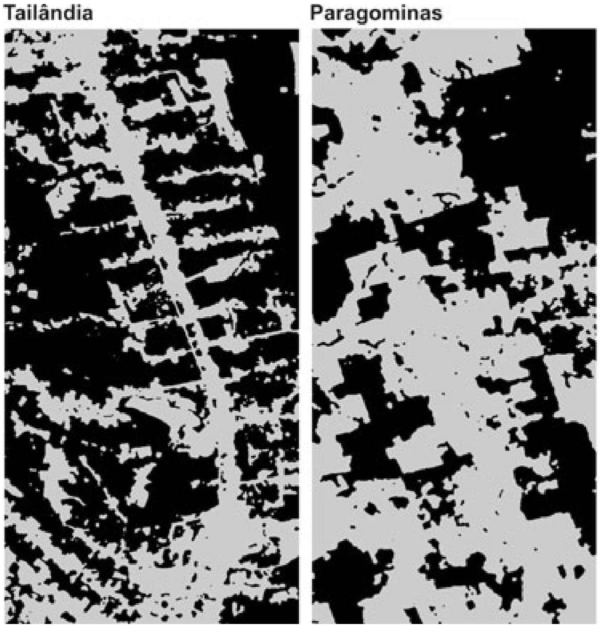

Fig. 1. Habitat fragmentation leads to a dramatic proliferation of forest edge, as shown in these two landscapes in eastern Amazonia (each 600 km^2 in area; dark areas are forest and light areas are mostly pastures).

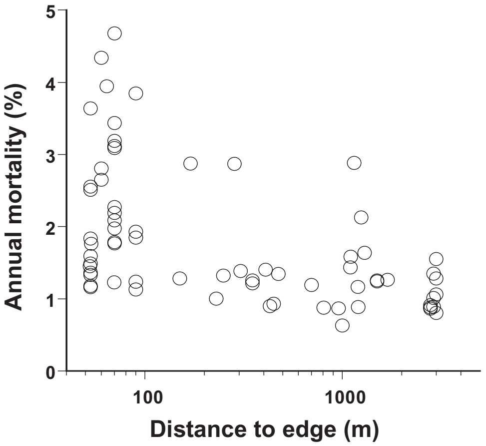

Fig. 2. Tree mortality often rises sharply near tropical forest edges. These data are from a long-term experimental study of forest fragmentation in central Amazonia (after Laurance *et al.* 1998a).

doi:10.1111/j.1442-9993.2008.01895.x

fragmented forests exhibit a marked decline in live biomass (Laurance *et al.* 1997), increased necromass and accelerated carbon cycling (Nascimento & Laurance 2004), and are probably a significant source of atmospheric carbon emissions (Laurance *et al.* 1998c).

FACTORS AFFECTING WIND DAMAGE

Complicating factors

The effects of wind on fragmented forests can be complicated by several factors. Damaging winds vary enormously in nature, from ephemeral wind gusts, to strong prevailing winds, to powerful cyclones and hurricanes, to brief but intense downdrafts from convectional thunderstorms (Nelson *et al.* 1994; Laurance 1997; McGregor & Nieuwolt 1998). Every cyclone or hurricane is in many senses unique, with a varying intensity, radius, forward speed and direction of movement (McGregor & Nieuwolt 1998; Turton 2008; Turton & Stork 2008). These complexities create much inherent spatial variability in wind damage, especially at the fragment and landscape scales.

Another complicating factor is local topography (Boose *et al.* 1994). Elevated and windward areas are generally most vulnerable to wind damage, whereas leeward and low-lying areas are usually least vulnerable. However, powerful winds can interact in complex ways with steep topography; for example, leeward areas can sometimes experience strong downwind turbulence (Turton & Stork 2008). Considerable damage to leeward-facing forests was evident during both Cyclones Rona and Larry, which struck north Queensland in 1999 and 2007, respectively (Grove *et al.* 2000; Turton 2008).

Life-history traits

Plants in environments that suffer recurring wind disturbance often possess functional traits that provide increased resistance or resilience to wind and these traits may influence their responses to fragmentation and edge effects (discussed below). Traits that provide increased resistance to wind damage include high wood density (Putz *et al.* 1983; Zimmerman *et al.* 1994; Curran *et al.* submitted, 2008a; Pohlman *et al.* 2008), stunted or low height (Schimper 1903; Grace 1977; Putz *et al.* 1983; Walker 1991; Pohlman *et al.* 2008), buttress roots (Elmqvist *et al.* 1994; Young & Perkocha 1994), low height : diameter ratio (Putz *et al.* 1983; van Gelder *et al.* 2006) and small stem diameter (Putz *et al.* 1983; Walker 1991; Franklin *et al.* 2004), although such traits do not confer resistance in all species or forest environments (e.g. Putz *et al.* 1983; Zimmerman *et al.* 1994; Bellingham *et al.* 1995; Ostertag *et al.* 2005; Curran *et al.* 2008a). Defoliation is another common consequence of intense winds, and may be reduced by traits such as low specific leaf area (Curran *et al.* 2008a; but see Bellingham *et al.* 1995) which reflects high leaf toughness (Wright & Cannon 2001). Despite its likely influence on wind-drag forces (Givnish 1979), leaf size (length or width) has not been found to influence defoliation (Bellingham *et al.* 1995; Curran *et al.* 2008a).

Unlike resistant species, plants that are resilient to wind damage recover quickly, either resprouting from snapped stems or damaged crowns, or regenerating via seeds or rapid growth of suppressed saplings. Resprouting is the most common mechanism in tropical forests, followed by sapling regeneration (Walker 1991; Bellingham *et al.* 1994; Zimmerman *et al.* 1994; Burslem *et al.* 2000). These mechanisms favour species with strong resprouting capacity and high growth rates, traits that are often negatively correlated with wood density (Putz *et al.* 1983; Curran *et al.* 2008b).

In general, species best adapted to withstand storms fall into two categories: slow-growing, resistant species with high wood density and structural strength, or fast-growing, resilient species with low wood density and rapid recovery from defoliation and stem damage (Lawton 1984; Ostertag *et al.* 2005; van Gelder *et al.* 2006; Curran *et al.* 2008b). These two life-history strategies are reflected in a range of plant functional traits (Table 1). It should be emphasized, however, that the two strategies are simply opposite ends of a spectrum. Despite a trade-off between many resistance and resilience traits, some species have intermediate traits or employ elements of both strategies (Bellingham *et al.* 1995). This is reflected, for instance, in a wide range of variation in wood density among species (Suzuki 1999; ter Steege & Hammond 2001; Muller-Landau 2004).

Landscape and fragment factors

Despite many potential complications, one can still make testable predictions about the expected influence of landscape and fragment structure on forest vulnerability to intense winds. First, other factors being equal, fragments surrounded by large clearings should be more vulnerable than those surrounded by small clearings. Large clearings have greater 'fetch' than small clearings, resulting in higher wind velocities and increased structural damage to adjoining forest stands (Somerville 1980; Savill 1983). Desiccation stress and temperature extremes are also likely to increase with clearing size (Malcolm 1998).

Second, small and irregularly shaped fragments should be more vulnerable to edge-related wind

doi:10.1111/j.1442-9993.2008.01895.x

Table 1. Expected functional traits in wind-resistant *versus* wind-resilient plant species

Trait	Explanation	Storm-resistant species	Storm-resilient species
Growth rate	Rate of biomass accumulation per unit time	Low	High
Resprouting capacity	Proportion of trees that resprout after stem snap	Low	High
Biomass accumulation from resprouting	Rate of biomass accumulation per unit time after stem snap	Low	High
Tree architecture	Height : diameter ratio; affects stability of the stem	Low	High
Wood density	Measure of the structural strength of stems and limbs, negatively correlated with growth rate	High	Low
Modulus of rupture	The force required to snap a stem of given thickness	High	Low
Modulus of elasticity	The stiffness (degree of deflection per unit force) before breakage	High	Low
Compression strength	Maximum amount of stress applied in compression without rupture or failure	High	Low
Specific leaf area (SLA)	Leaf area per unit mass, also considered an index of sclerophylly (low SLA = sclerophyllous leaves). Low-SLA leaves are tougher but associated with slow growth rates; high SLA facilitates rapid growth but leaves are weaker.	High	Low

damage than are larger or more-circular fragments, which have a lower ratio of perimeter to edge (Laurance & Yensen 1991). Many edge effects appear to be additive in nature, such that an area of forest influenced by multiple nearby edges will suffer greater edge effects than one influenced by just a single nearby edge (Malcolm 1994, 1998). On the Atherton Tableland in north Queensland, this phenomenon probably contributed to intense forest structural damage and a proliferation of disturbance-adapted plants in rainforest fragments, relative to nearby intact forest, following Cyclone Winifred in 1986 (Fig. 3; Laurance 1991).

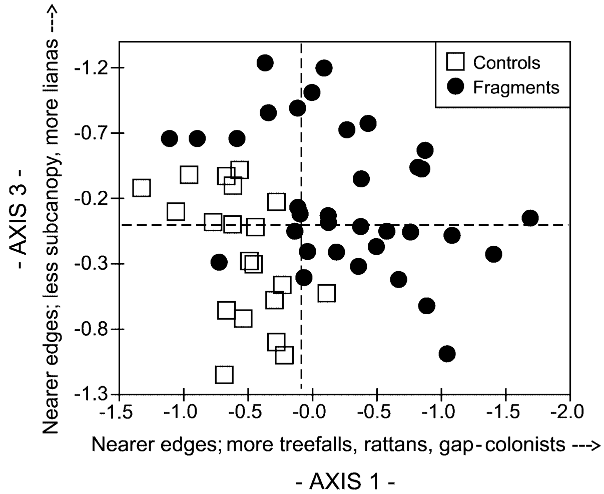

Fig. 3. As demonstrated by this ordination analysis, rainforest fragments in north Queensland (ranging from 1.4–590 ha in area) had heavier structural damage and more disturbance-adapted plants than did nearby intact forest (controls), following Cyclone Winifred in 1986 (after Laurance 1991).

Third, edge structure may influence vulnerability to wind disturbance. In the tropics, newly formed edges (<5 years old) are structurally open and thus more permeable to lateral light and hot, dry winds than are older edges, which tend to become 'sealed' by a proliferation of vines and secondary growth (Kapos *et al.* 1993; Camargo & Kapos 1995; Didham & Lawton 1999). Wind damage, however, may actually increase as fragment edges become older and less permeable (but see Pohlman *et al.* 2008), because wind-tunnel models suggest that downwind turbulence should increase when edge permeability is reduced (Savill 1983). For these reasons it is plausible that tree mortality from microclimatic stress will be greatest near newly formed edges, whereas wind-related mortality will be more important near older edges. This accords with findings in central Amazonia, where many undamaged trees die (evidently from physiological stress) near newly formed edges (Lovejoy *et al.* 1986), whereas windthrow and trunk-snapping are the most important cause of tree mortality near older edges (D'Angelo *et al.* 2004). Land-use practices that repeatedly disturb fragment margins (such as regular burning of adjoining pastures) can have a large influence on the nature and intensity of edge effects, by preventing natural edge closure (Cochrane *et al.* 1999; Gascon *et al.* 2000).

Fourth, edge orientation (aspect) is often important, especially during intense storms, because it can greatly influence the exposure of the edge to wind shear. Canopy cover was negatively correlated with an index of increasing exposure to cyclonic winds in rainforest fragments on the Atherton Tableland, following Cyclone Winifred in 1986 (Laurance 1991). While both edge aspect and topographic position were encapsulated in this index, the results clearly demonstrated that west-facing edges, which bore the brunt of the cyclonic winds, experienced the greatest canopy-cover loss. Similarly, soon after Cyclone Larry in 2006, forest structural damage (canopy loss, treefalls, limb breakage) in rainforest fragments on the Atherton Tableland was strongly affected by edge aspect (Curran *et al.* submitted). Edges that directly faced the cyclonic winds (west and northwest) were most heavily damaged, whereas those with opposite aspects (east and southeast) were least damaged and those partially exposed to the cyclone (southwest, north, northeast and south) had intermediate damage. Notably, edge aspect can also influence other aspects of forest ecology. For example, heat and desiccation stress are highest on edges facing the afternoon sun (Turton & Freiberger 1997; Malcolm 1998), whereas atmospheric deposition of wind-borne pollutants and nutrients is greatest on edges that face prevailing winds (Weathers *et al.* 2001).

Finally, the structure of the modified vegetation surrounding fragments can clearly affect forest-climate interactions. In the Amazon, fragments surrounded by regrowth forest are partially buffered from damaging winds and harsh external microclimates, and suffer lower edge-related tree mortality than do those encircled by cattle pastures (Fig. 4; Mesquita *et al.* 1999). Likewise, in north Queensland, forest edges adjoined by regrowth tended to have less structural damage than those without regrowth (Laurance 1997). Regrowth bordering forest margins can also strongly influence the intensity of edge-related microclimatic gradients (Kapos *et al.* 1993; Camargo & Kapos 1995; Didham & Lawton 1999).

WIND-FRAGMENTATION SYNERGISMS

Wind disturbances – especially recurring disturbances – could exacerbate some of the ecological impacts of forest fragmentation. Under some circumstances, winds might even interact synergistically with fragmentation, leading to unexpectedly severe and unanticipated effects (cf. Laurance & Cochrane 2001; Laurance & Peres 2006). Here we highlight four categories of environmental change in fragmented forests that could be markedly worsened by wind disturbance.

Altered forest structure and biomass

As discussed above, fragmented tropical forests are vulnerable to a wide range of physical and biotic edge effects, even in regions like the Amazon (e.g. Fig. 2) where wind disturbance is limited to prevailing winds and occasional windblasts from convectional thunderstorms. In cyclonic and hurricane zones, the damage from destructive winds can be far more intense. Rainforest fragments in north Queensland affected by Cyclones Winifred (Fig. 4) and Larry (Fig. 5), for example, were often exceptionally disturbed, with a heavy loss of canopy cover, frequently severe structural damage to all vertical levels of the forest, and a proliferation of light-loving plant species in the forest understorey. It seems likely that the marked loss of live biomass in Amazonian forest fragments (Laurance, Laurance *et al.* 1997) – which is driven both by heavy tree mortality (Laurance *et al.* 1998a, 2000) and by a shift towards fast-growing tree and liana species with relatively low wood density, and thus low carbon storage (Laurance *et al.* 2001, 2006a, 2006b) – will be even more exaggerated in cyclone-disturbed forests. The net effect will be not only hyper-disturbed forest

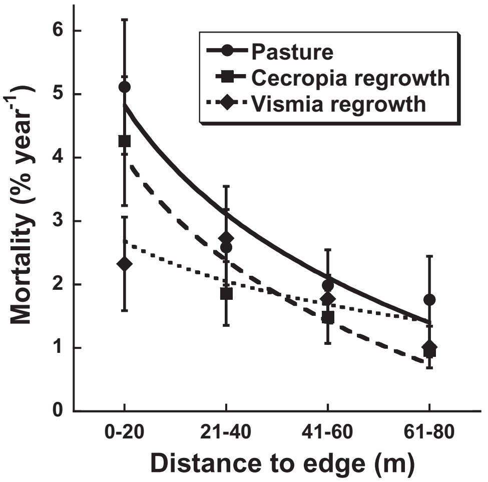

Fig. 4. Effects of adjoining vegetation on edge-related tree mortality in Amazonian forest fragments (after Mesquita *et al.* 1999).

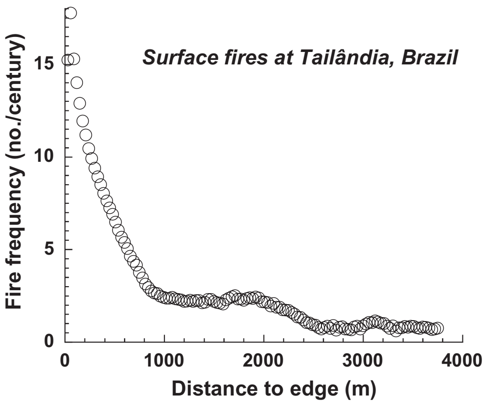

Fig. 5. Dramatic increase in the incidence of fire in fragmented forests in eastern Amazonia, as a function of distance from fragment margins. The fire-frequency curve is the mean for several hundred forest fragments, averaged over a 14-year period (after Cochrane & Laurance 2002).

remnants (Laurance 2002), but also substantially reduced carbon storage in fragmented forests (cf. Nascimento & Laurance 2004). Such reductions in carbon storage could be an important source of greenhouse gas emissions, perhaps totaling up to 150 million tons of atmospheric carbon emissions annually, based on current rates of forest loss and fragmentation in the tropics (Laurance *et al.* 1998c).

Species invasions

Forest fragments are vulnerable to invasions from exotic and generalist species that proliferate in the matrix of modified habitats surrounding fragments, and which can generate a heavy seed rain into fragments (Janzen 1983; Laurance 1991; Viana *et al.* 1997; de Melo *et al.* 2006; Nascimento *et al.* 2006). Fragments are even more vulnerable to such invasions following major canopy damage from cyclones or hurricanes. On the Atherton Tableland, exotic and disturbance-loving plant species (e.g. lianas, *Solanum* spp., *Dendrocnide* spp., *Calamus* spp., *Neolitsea dealbata*) proliferate extensively in the understories of cyclone-disturbed rainforest fragments (Laurance 1991, 1997). Such species are favoured by high light levels in the forest understorey following wind disturbance (Bellingham *et al.* 1996; Horvitz *et al.* 1998). Dense profusions of light-loving vines, such as *Calamus* spp., can dominate lowland forests in north Queensland that suffer recurring cyclone disturbance (Webb 1958). Similarly aggressive plant invasions have been observed in storm-damaged forest remnants in Polynesia (Wiser *et al.* 2002) and Madagascar (Brown & Gurevitch 2004). In Jamaica, cyclone disturbance has accelerated the invasion of native forests by the exotic tree *Pittosporum undulatum* (Bellingham *et al.* 2005). Clearly, heavy canopy disturbance from winds can make fragmented forests increasingly vulnerable to exotic-species invasions.

Changes in plant species composition

Wind disturbance may exacerbate and possibly alter fragmentation-related changes in plant communities. In general, canopy damage from winds will provide even greater advantages for lianas, climbing rattans and other vines, which favour disturbed (Putz 1984) and fragmented (Viana *et al.* 1997; Laurance *et al.* 2001) forests. Lianas are important structural parasites of trees that can suppress tree regeneration, increase mortality and reduce tree growth and reproduction (Putz 1984; Viana *et al.* 1997; Schnitzer & Bongers 2002).

The impacts of wind damage on fragmented tree communities may depend in part on the natural disturbance regime of the forest. In central Amazonia, where large-scale wind disturbance is naturally rare (Nelson 1994; Nelson *et al.* 1994), fragmentation causes remarkably rapid changes in tree communities, favouring fast-growing early successional trees with low wood density, small seeds, abiotic seed dispersal and low shade tolerance (Laurance *et al.* 1998b, 2006b; Tabarelli *et al.* 1999). Many old-growth species, especially slow-growing, shade-tolerant subcanopy trees that have obligate outbreeding and rely on mammals or larger birds for seed dispersal, are especially disadvantaged (cf. Laurance *et al.* 1998a, 2006a, 2006b; Gillespie 1999; Moran *et al.* 2004; White *et al.* 2004; de Melo *et al.* 2006; Muñiz-Castro *et al.* 2006).

In regions such as the cyclonic and hurricane zones where major wind disturbance is more frequent, tree communities are likely to have shifted in composition to favour disturbance-resistant and -resilient species (Table 1). In this context, we believe that fragmentation might further increase the abundance of disturbance-resilient species, whose life history strategies (rapid growth, light-loving, low wood density, rapid resprouting after stem damage) will generally be favoured by edge effects and recurring canopy disturbance. Some species adapted to resist wind damage (slow-growing, high wood density, stiff stems, wind-resistant architectures) may decline in abundance, especially if fragments are so heavily or chronically disturbed that their capacity to tolerate such disturbances is overwhelmed. For example, small (<76 ha) fragments of tropical dry forest in Puerto Rico had comparable damage to nearby intact forests following a category-3 hurricane, but suffered an unusually high incidence of uprooted trees, especially among larger size-classes (Van Bloem *et al.* 2005), and many of these would be unlikely to recover. The relative success of wind-resistant and -resilient species might be mediated in part by their reproductive biology; for example, rapid growth (typical of disturbance-resilient species) tends to be positively correlated with small seed size and high fecundity (Foster & Janson 1985), which are generally advantageous in disturbed and fragmented forests (Moran *et al.* 2004; White *et al.* 2004; de Melo *et al.* 2006; Laurance *et al.* 2006a). We emphasize that these predictions are merely informed speculation, and require testing with field data.

Increased vulnerability to fire

One of the most alarming consequences of forest fragmentation is a drastic increase in the incidence of fire. Large, intact forest tracts very rarely burn, because they have few ignition sources and because the high humidity of the forest facilitates rapid decomposition

doi:10.1111/j.1442-9993.2008.01895.x

of litter and organic material, keeping fuel loads at a minimum (Cochrane *et al.* 1999). When landscapes are fragmented, however, surviving forests are often surrounded by fire-maintained pastures or slash-and-burn farming plots, creating ready sources of ignition. In the Amazon, for example, ranchers burn their pastures annually to control weeds and to promote a flush of green grass for cattle, and these fires often penetrate into adjoining forest fragments. Fragmentation also promotes forest desiccation, canopy damage and litter accumulation near fragment margins (Kapos 1989; Didham & Lawton 1999), which further increases forest flammability. The fire-fragmentation synergism (Fig. 5) is especially striking in relatively seasonal areas of tropics, where dry-seasons are pronounced, and in the vast areas of the Asian-Pacific, Australian and Neotropical regions that experience El Niño droughts (Laurance & Williamson 2001; Cochrane & Laurance 2002).

Fragmented forests damaged by wind could be especially vulnerable to fire, because they will have greater canopy damage and more flammable debris in the forest understorey. To evaluate this possibility we recorded canopy cover as well as mean leaf-litter depth, fine-wood debris (pieces 1–5 cm in diameter), and climbing-rattan (*Calamus* spp.) abundance within 2 m of the ground within three cyclone-damaged forest fragments (6.3, 41 and 75 ha in area) on the southern Atherton Tableland. Data were recorded within 22 randomly positioned plots in December 2006, 9 months after Cyclone Larry. Within each plot, canopy cover was estimated as the mean of four spherical densiometer measurements taken at cardinal directions. Wood debris and rattan-stem abundance were quantified using the planar-intercept method (cf. Nascimento & Laurance 2004) along two 5-m long planes, situated at right angles within the plot. Litter depth was the mean of 11 measurements, recorded at 1-m increments along the two planes.

Using linear regressions, we found that canopy cover was an excellent predictor of fine-wood debris (Fig. 6) ($F_{1,20} = 25.23$, $R^2 = 56.1\%$, $P = 0.0001$) and litter depth ($F_{1,20} = 11.36$, $R^2 = 36.2\%$, $P = 0.003$), but not rattan abundance ($F_{1,20} = 0.01$, $R^2 = 0.4\%$, $P = 0.93$), which was highly patchy (rattan abundance probably reflected canopy openings caused by previous disturbance events, rather than the recent cyclone). Given the intense canopy disturbance suffered by many forest fragments and edges during Cyclone Larry (Curran *et al.* submitted; Turton & Stork 2008), these findings strongly suggest that fine-fuel loads rose sharply within damaged fragments. The loss of canopy cover, which allows light and wind to penetrate to the forest floor, would also increase fuel desiccation and flammability. In the case of Cyclone Larry, major forest fires may only have been prevented by very heavy rainfall in the months immediately following the cyclone. These rains both precluded ignition and promoted rapid decomposition of the remarkably heavy litter that had accumulated on the forest floor, following widespread defoliation of trees by the cyclone (Turton & Stork 2008).

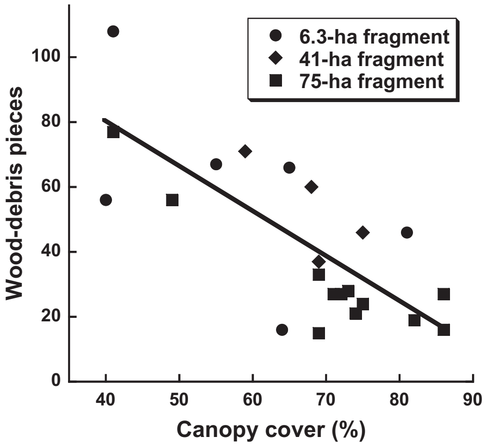

Fig. 6. Relationship between forest-canopy cover and the abundance of fine-wood debris (number of pieces 1–5 cm in diameter) in three cyclone-damaged rainforest fragments in north Queensland.

Hence, the situation following Cyclone Larry was fortunate, because favourable weather prevented large-scale forest fires. In other circumstances, storm-damaged forests will be increasingly likely to burn, especially when fragmented. In general, rainforest vegetation is poorly adapted to fire, lacking adaptations such as thick bark and lignotubers that permit fire-adapted species to survive burning (Cochrane & Laurance 2002), although post-fire resprouting is not uncommon among species in drier rainforests and forest ecotones (Unwin *et al.* 1985; Uhl & Kauffman 1990; Cochrane 2003). A particularly alarming consequence of rainforest fires is that they tend to be self-promoting: the initial fire kills many trees and most vines and forbs, and as these die the canopy thins and more litter accumulates on the forest floor. The concentration of dry, flammable fuel means that subsequent fires are much more intense and destructive, and this positive-feedback process frequently continues until the rainforest has been destroyed (Cochrane *et al.* 1999; Cochrane 2003). Hence, windstorms could potentially worsen an already alarming synergism between fragmentation and fire, with potentially dire consequences for some tropical forests.

ACKNOWLEDGEMENTS

We thank Steve Turton for comments on the manuscript; Robert Ewers, Andy Jones, Magdalena Vinson, and Ellen Reid for assistance with fieldwork; and the

doi:10.1111/j.1442-9993.2008.01895.x

National Geographic Society, CSIRO Tropical Forest Research Centre, School for Field Studies, and Smithsonian Tropical Research Institute for financial and logistical support.

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