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Recruitment dynamics of invasive species in rainforest habitats following Cyclone Larry

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Abstract In tropical forests, natural disturbance creates opportunities for species to claim previously utilized space and resources and is considered an important mechanism in the maintenance of species diversity. However, ecologists have long recognized that disturbance also promotes exotic plant invasions. Cyclones cause extensive defoliation, loss of major branches and multiple tree falls, resulting in a significantly more open canopy and increased light and heat levels in the understorey. The widespread and massive disturbance caused by cyclones provides ideal conditions for rapid recruitment and spread of invasive species. The ecological roles of invasive species in rainforest habitats following such a severe disturbance are poorly understood. Severe category 4 Cyclone Larry crossed the North Queensland coast in March 2006 causing massive disturbance to rainforest habitats from Tully to Cairns and west to the Atherton Tablelands. We established 10 plots in an area extensively damaged by this cyclone near El Arish in North Queensland. On each plot nine 2 × 2 m quadrats were established with three quadrats per plot in each of the following treatments: (i) complete debris removal down to the soil layer, (ii) removal of coarse woody debris only, and (iii) uncleared. We monitored recruitment, growth and mortality of all native and invasive species in the 90 quadrats every 3 months since the cyclone. Here we present the recruitment dynamics of invasive species across the study area in relation to the level of disturbance, the type of quadrat treatment, and the diversity and abundance of the native recruiting flora over the first 12 months post-cyclone. Our results suggest that invasive species will mostly comprise a transient component of the flora in the early stages of the successional response. However, some species may have longer-term effects on the successional trajectory of the rainforest and future forest composition and structure.

Key words: cyclone, invasive, rainforest, recruitment, succession, weed.

INTRODUCTION

In tropical areas, most studies have focussed on the role of small-scale disturbances and gap dynamics in determining forest composition and structure (Denslow 1987; Hubbell *et al.* 1999). However, emerging evidence shows that large-scale and infrequent disturbances such as cyclones or hurricanes may dominate tropical forest dynamics and shape forest diversity, composition and structure (Burslem & Whitmore 1999; Debski *et al.* 2000; Baker *et al.* 2005; Tanner & Bellingham 2006). Large-scale disturbances create a heterogeneous environment and release growing space, generating opportunities for the recruitment of seedlings and the release from competition of more advanced plants from which the forest stand develops. Widespread disturbances can create discrete temporal pulses of establishment which are evident in structural and floristic composition of tropical forests tens to hundreds of years later (Baker *et al.* 2005).

The seedling recruitment phase is a point of major constriction in the population dynamics of many species (Hille Ris Lambers & Clark 2003; Connell *et al.* 2005; Uriarte *et al.* 2005) and influences community diversity, composition and structure of tropical forests in the long-term (Harms *et al.* 2000). However, while there is a significant literature on changes in forest structure caused by wind damage to existing trees, there is very little empirical research on seedling recruitment dynamics following cyclones (but see Guzmán-Grajales & Walker 1991; Horvitz & Koop 2001). In part, this is due to the practical difficulties associated with observing seedling recruitment and identifying species at the seedling stage and, since cyclones themselves are relatively rare, the low probability of encountering such a disturbance.

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Cyclones can alter many of the processes that may determine the number of seedlings that recruit into a given area. Cyclones cause extensive defoliation, loss of major branches and multiple tree falls resulting in a significantly more open canopy (e.g. Metcalfe *et al.* 2008). The spatial extent and distribution of gaps following severe cyclones results in a landscape that is distinct from that associated with small-scale tree falls; gaps are much larger and interconnected and surrounding vegetation is also damaged (Horvitz *et al.* 1998). Cyclone damage to tree crowns may decrease or delay seed production in the short term e.g. up to 6 months (Walker & Neris 1993; M.G. Bradford, D.J. Metcalfe, pers. comm. 2007) or result in increased fecundity of understorey species (Hopkins & Graham 1987). Consequently, there may be a long lag time in recovery, to pre-cyclone levels, of seed sources at a landscape level. Light and heat levels increase dramatically in the understorey and this may have both negative and positive effects depending on particular species' traits (Yamashita *et al.* 2000; Walker *et al.* 2003). Increased light and heat may kill seeds before germination and desiccate existing seedlings or stimulate seed germination and growth (Guzmán-Grajales & Walker 1991; Walker *et al.* 2003). Negative effects are also caused by increased litter inputs, which may kill seedlings already present, or inhibit germination by covering seeds and preventing seedling establishment (Metcalfe & Turner 1998; Uriarte *et al.* 2005). Litter inputs may also enhance nutrient supply with positive effects on growth (Walker *et al.* 2003).

The widespread and massive disturbance caused by cyclones provides ideal conditions for rapid recruitment and spread of invasive species. The ecological roles of invasive species in rainforest habitats following severe disturbances are very poorly understood. Some research has shown that hurricanes and cyclones accelerate invasions and alter the abundance of non-indigenous species in tropical forests (e.g. Merlin & Juvik 1995; Horvitz *et al.* 1998; Bellingham *et al.* 2005). Invasive species can alter the successional trajectory of forest recovering from large-scale disturbance by reducing colonization success of native species. This may result from site saturation by invader propagules or recruits which take up available germination sites and space. These potential effects of invasion may become magnified in systems already limited by dispersal of native species propagules, but where propagule pressure from invading species is enhanced by the disturbance.

There are now over 200 exotic plant species listed as having naturalized at some time in the rainforest habitats of Queensland (Metcalfe & Ford 2007). The compounded effects of an increasing number and diversity of invasive species in tropical habitats and the possibility of an increasing frequency of intense cyclones as a result of changing climatic conditions (Knutson & Tuleya 2004; Webster *et al.* 2005) may result in significant and relatively rapid changes to forest composition, diversity and structure. Managing and adapting to these changes requires an understanding of how native and invasive species interact and compete during the recruitment phase.

Severe category 4 Tropical Cyclone Larry (maximum wind gusts at landfall >290 km h^{-1}) crossed the North Queensland coast of Australia on Monday 20 March 2006 causing massive disturbance to rainforest habitats from Tully to Cairns and west to the Atherton Tablelands (see Turton 2008). In the period 1858 to 2006, 41 cyclones crossed the wet tropical coast of Queensland with four having notable impact on the study area (Turton & Stork 2008). The last major cyclone to affect our study area before Larry was Category 3 Cyclone Winifred in 1986 (maximum wind gust approximately 200 km h^{-1}; Beach Protection Authority, 1986). Over the past year we have monitored recruitment, growth and mortality of all native and invasive species in an area extensively damaged by Cyclone Larry.

Here we present the recruitment dynamics of invasive species across the study area in relation to the level of disturbance, the debris load and the abundance and diversity of the native recruiting flora. We set out to test the hypothesis that invasive species will show increased recruitment in tropical forest communities where (i) cyclone damage is highest, (ii) native species richness and/or diversity is lowest, and (iii) litter and debris do not present a barrier to recruitment.

METHODS

Study site

The study site is located 1 km west of the township of El Arish, in North Queensland (–17°48′, 145°59′) (Fig. 1). The site is partly located on private property and extends into Japoon National Park and the Wet Tropics World Heritage Area. Vegetation at the site has been mapped as 7.11.1a Simple-complex Mesophyll Vine Forest by the Queensland Government Environmental Protection Agency (2006). The area has previously been logged and the disturbance caused by the logging is evident in the presence of stumps and the remnants of access trails through the area. Average annual rainfall at El Arish is 3733 mm, most of this falling in the summer months (January to March). The geology is of metasedimentary origin with a landform of moderately inclined to steep slopes. Three permanent creeks traverse the area.

The area in which the study site was established was extensively damaged by cyclone Larry. The eye of the cyclone crossed the coast approximately 25 km north

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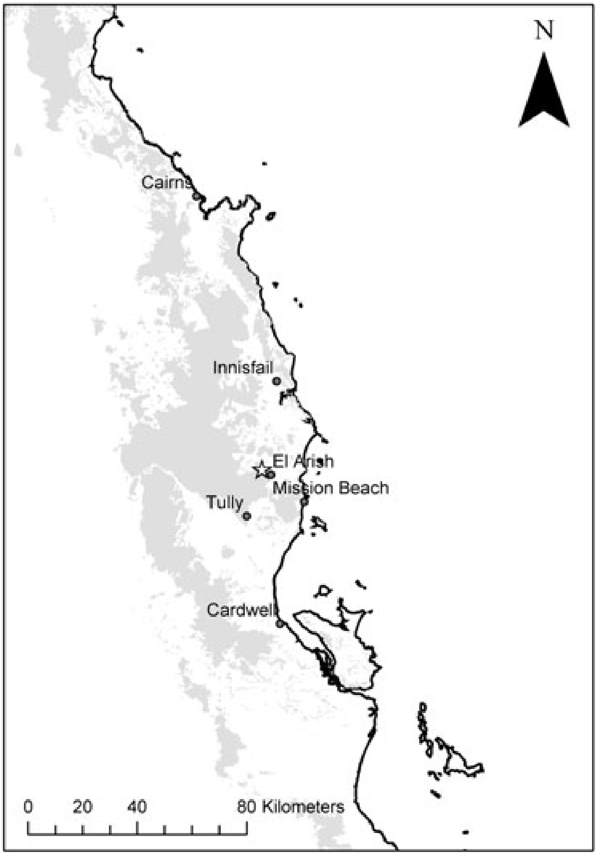

Fig. 1. Study site location (☆). Forested areas are shown in grey.

of the site. Maximum wind gusts experienced at the site were likely up to 290 km h^{-1} (Bureau of Meteorology 2007). East facing slopes were more extensively damaged than west facing slopes.

The study site is located in an area actively managed by the Biosecurity Queensland, Four Tropical Weeds Eradication Program for *Miconia calvescens* (Melastomataceae), a declared Class 1 weed species (Land Protection (Pest and Stock Route Management) Act 2002). Tracks maintained through the area as part of the eradication programme allowed access to areas of rainforest that would have been virtually inaccessible following the cyclone.

Plots and quadrats

Ten 50 × 20 m plots were established in the study site (Fig. 1). The distance between the two most distant plots was approximately 1 km. Plots were located to encompass the range of damage conditions in the area. Damage was assessed by means of the Bradford–Unwin Damage Scale (Metcalfe *et al.* 2008) adapted from Unwin *et al.* (1988). In each plot, all surviving trees $\geq$10 cm d.b.h. were measured (height and d.b.h.) and identified. Plots were located in areas with Bradford–Unwin damage scores of 1.5 – 'severe and common disturbance' (5 plots); 2 – 'severe and localized disturbance' (2 plots); 2.5 – 'moderate disturbance' (2 plots); and 3 – 'moderate to slight disturbance' (1 plot).

In each plot, nine 2 × 2 m quadrats were established (total of 90 quadrats). Three quadrats were assigned to each of three litter treatments: (i) uncleared, that is, no treatment; (ii) partially cleared, with only coarse woody debris removed (i.e. all woody debris with diameter greater than approximately 2 cm); and (iii) fully cleared of leaf litter and debris down to the soil layer. Quadrats were generally laid out in lines so that three quadrats (one of each treatment) were established in a line running down each end of the plot on the long axis, with one line running down the middle (i.e. at 0, 25 and 50 on the long axis). Quadrats were marked in each corner with wooden posts. Plots and quadrats were established between 5 and 12 weeks after the cyclone.

Surveys

All native and invasive angiosperm (excluding some common ground herbs e.g. *Pseuderanthemum variabile*) in each quadrat were labelled with a numbered aluminum tag. The tag for seedlings <3 cm in height was usually placed on a small steel stake at the base of the plant. Occasionally a flush of seedlings from one species dominated recruitment in a quadrat. When seedlings were too numerous or densely packed to tag individually, we counted seedlings of the particular species in four 1 × 1 m subquadrats. In subsequent surveys the number of seedlings in each of the subquadrats was recounted so a mortality index could be generated and, if feasible, recruits that had survived were then tagged individually.

We identified all seedlings to genus or to species wherever possible and estimated their height. At each survey period, all tags were relocated, the identification confirmed and the height (or mortality) recorded. Tags that were not relocated on two consecutive visits were recorded as 'not found'. 'Not found' tags mostly result from vertebrate digging or very heavy rainfall occasionally dislodging tags and stakes so that the original location of the plant could not be confirmed. All newly emerged seedlings were tagged, identified and the height recorded at each survey. Leaf litter was removed from fully cleared quadrats at each survey period.

The second survey took place approximately 6 weeks after the initial quadrat set-up. Monitoring was then conducted approximately every 3 months. Results reported here are for the first year following

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the cyclone, that is, initial set-up (first survey) (S1), second survey (S2), third survey (S3) and fourth survey (S4).

Analysis

Simpson's diversity index (D) for native species was calculated for all quadrats as:

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

Where S is the total number of native species in the community and p_i is the proportion of a given species (i) relative to S. Individuals that could not be identified to species were not included in the species diversity measure.

Mortality for each species in each plot was calculated by dividing the total number of seedlings that died over the study period by the total number present through the study period.

Pearson correlation coefficients were calculated to examine the relationship between the total number of native species and native species diversity in quadrats and total number of invasives in quadrats at each survey period. Univariate GLM was used to determine the main and interaction effects of litter treatment and plot damage level on native and invasive species recruitment. Tukey's *post hoc* tests were then conducted on significant effects.

RESULTS

A total of 15 091 individual seedlings were recorded over the study period, of which 1381 (9.1%) were invasive. A total of 854 individuals (5.6%) could not be identified to either genus or species. A total of 241 species from 79 families were recorded, of which 11 (from five families) are invasive. The four most common native species' families recorded were Lauraceae (19 species), Rubiaceae (13 species), Sapindaceae (11 species) and Euphorbiaceae (10 species). Thirty-six families were represented by a single species. *Crassocephalum crepidioides* (Asteraceae) was the most abundant invasive, making up 70% (971) of invasive individuals (Table 1) and occurring in 78 of the 90 quadrats. Invasive species were over-represented by herbs and shrubs compared with the native flora (invasive herbs 45% compared with native 3.3%; invasive shrubs 45% compared with native 12%) and under-represented by trees and vines (one tree species among the invasives compared with 55% native tree species and 24% native vine species).

Only 11 of the 90 quadrats contained no invasives. The number of invasive individuals in quadrats was significantly positively correlated with the number of native individuals at all survey periods (Table 2). Number of invasive individuals was significantly, though weakly, negatively correlated with native species diversity in quadrats in survey periods 2 and 3.

Univariate GLM indicates a significant effect of both litter treatment ($f = 4.537$, $P < 0.05$, d.f. = 2) and damage level ($f = 5.982$, $P < 0.001$, d.f. = 3) on the number of invasive species in quadrats, but no interaction effect ($f = 1.001$, $P > 0.05$, d.f. = 6). The same analysis showed no significant effect of either litter treatment ($f = 0.387$, $P > 0.05$, d.f. = 2), damage level ($f = 0.950$, $P > 0.05$, d.f. = 3) or any interaction of the two on the number of individuals of native species in quadrats. Invasives were most abundant in the most severely damaged plots (damage score 1.5) and in the fully cleared quadrats (Fig. 2; Table 3). *Post hoc* test shows the mean number of invasives in fully cleared quadrats is significantly larger than in partly cleared or

Table 1. Invasive species, total individuals of each species, total number of quadrats the species occurs in and mean mortality over the study period

Species	Family	Life form	Total individuals	No. of quadrats	Mean mortality
Ageratum conyzoides subsp. conyzoides	Asteraceae	Herb	154	21	0.20
Crassocephalum crepidioides	Asteraceae	Herb	971	78	0.41
Emilia sonchifolia	Asteraceae	Herb	33	12	0.36
Erechtites valerianifolius forma valerianifolius	Asteraceae	Herb	22	17	0.34
Miconia calvescens	Melastomatceae	Tree	13	7	0.00
Praxelis clematidea	Asteraceae	Herb	2	1	0.00
Rubus alceifolius	Rosaceae	Scrambling shrub	175	41	0.22
Solanum capsicoides	Solanaceae	Shrub	1	1	0.00
Solanum mauritianum	Solanaceae	Shrub	3	3	0.00
Solanum torvum	Solanaceae	Shrub	5	5	0.00
Spermacoce mauritiana	Rubiaceae	Shrub	1	1	0.00

Table 2. Pearson correlation coefficients between the number and diversity of native species and the number of invasive species individuals in quadrats ($n = 90$) at each survey period (S1–S4)

Survey period	S1	S2	S3	S4
Native species number	0.303**	0.505***	0.479***	0.383***
Native species diversity	–0.081	–0.236*	–0.212*	–0.151

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

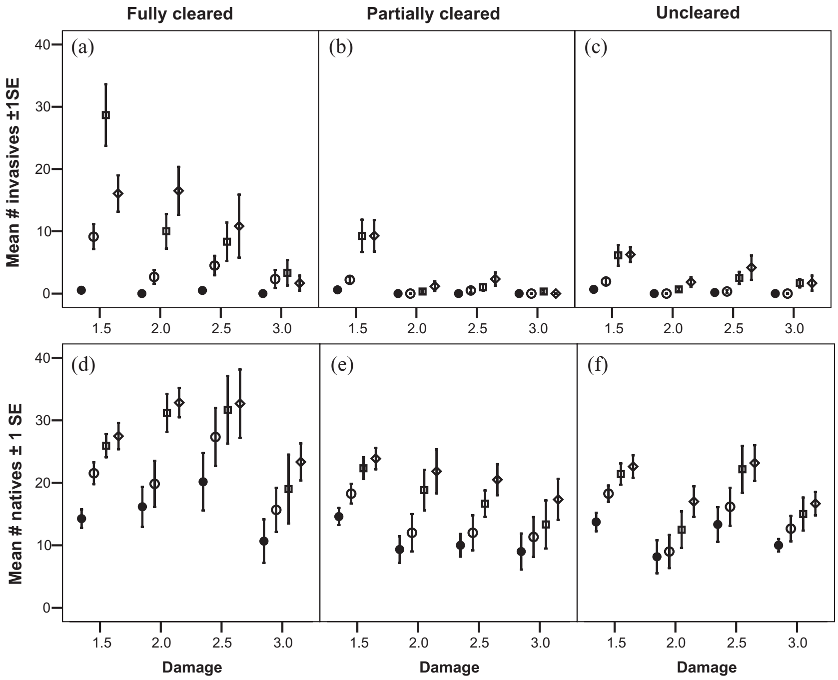

Fig. 2. Mean number of invasives in (a) fully cleared, (b) partially cleared and (c) uncleared quadrats, and mean number of native species in (d) fully cleared, (e) partially cleared and (f) uncleared quadrats over the four surveys (●) first survey, (○) second survey, (□) third survey, (◇) fourth survey, at plots with different levels of cyclone damage.

uncleared quadrats at all damage levels except for in the least damaged plot (damage score 3) (Table 3). For native species the effect of litter treatment was only evident in the most severely damaged plots (damage score 1.5) where fully cleared quadrats contained more individuals on average than uncleared quadrats (Table 3).

Mortality of invasive herb species over the study period was relatively high (Table 1). The scrambling shrub *Rubus alceifolius* also had relatively high mortality while the remainder of the invasive shrubs and tree species showed no mortality over the study period, though their overall numbers were much lower (Table 1). Of the native species, mean mortality was highest among the vines (15%), followed by shrubs (8%), trees (7%) and herbs (5%). At the higher damage levels, mean mortality of invasive herbs is generally lowest in the fully cleared quadrats (Fig. 3).

DISCUSSION

Invasive species in this community capitalized to a greater extent than the native species on the disturbance created by Cyclone Larry. Invasives are most abundant in the most severely damaged plots and on the fully cleared quadrats. Native species abundance tends to be more consistent across damage levels and litter treatments. However, the positive correlations between native and invasive species number in quadrats indicate that, to some extent, sites that are most favourable for recruitment of invasives are also favourable for recruitment of native species.

Guzmán-Grajales and Walker (1991) found highest seedling densities in a similar litter removal treatment following Hurricane Hugo in Puerto Rico, and suggested litter is a major constraint to recruitment of seedlings following such a disturbance. However, that work also showed that species responded differentially

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Table 3. Results of *post hoc* analysis of differences in mean number of invasive and native species occurring in the three litter treatments (F – fully cleared, P – partially cleared, U – uncleared) within each damage level

	Invasives			Natives		
Treatment	*P*	Mean	SE	*P*	Mean	SE
Damage score 1.5 (*n* = 15)	0.002			0.028		
F		44.0^{a}	10.67		155.4^{a}	22.33
P		18.1^{b}	4.25		115.6^{a,b}	27.38
U		9.8^{b}	2.04		73.1^{b}	7.6
Damage score 2.0 (*n* = 6)	0.000			0.864		
F		20.16^{a}	4.23		194.8	73.5
P		1.33^{b}	0.95		138.0	66.5
U		2.17^{b}	0.98		150.3	91.0
Damage score 2.5 (*n* = 6)	0.025			0.643		
F		14.83^{a}	4.68		141.3	35.2
P		2.83^{b}	1.05		247.3	161.2
U		4.83^{b}	1.74		129.3	23.2
Damage score 3.0 (*n* = 3)	0.26			0.838		
F		4.33	2.03		141.0	11.5
P		0.33	0.33		181.6	47.5
U		3.33	1.85		175.6	74.4

Values with different superscript within trios are significantly different ($P < 0.05$).

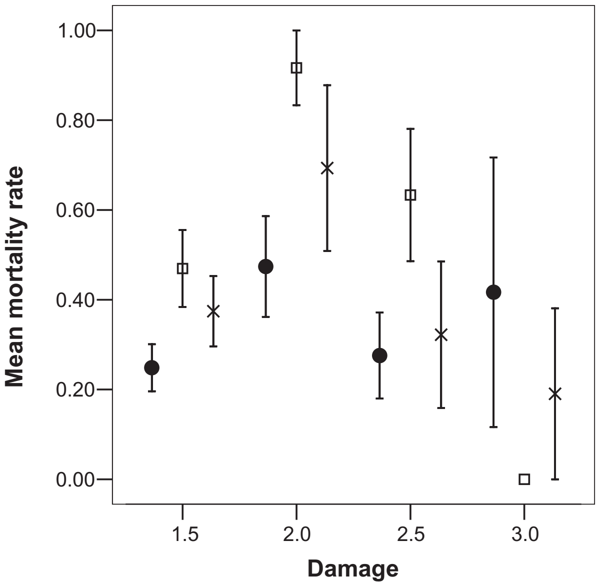

Fig. 3. Mean mortality of invasive herbs with four damage levels and litter treatment (●) fully cleared, (□) partially cleared, and (×) uncleared quadrats.

to the treatment. Species characteristic of early succession were most abundant in the litter removal treatment while species characteristic of later successional stages either did not increase or declined in abundance in that treatment. Metcalfe and Turner (1998) also found that litter removal enhanced germination under a closed forest canopy, but while small-seeded species were favoured by litter removal, intermediate and large-seeded species were not significantly affected. Modification of light and temperature conditions by litter may favour germination of later successional and shade-tolerant species. Guzmán-Grajales and Walker (1991) found litter removal was detrimental to germination and growth of the large-seeded, shade-tolerant species, *Dacryodes excelsa*, that dominates mature stands in their study area. This result is consistent with our finding that invasive species (which are typically early successional owing to their low tolerance of shade) recruit more readily into quadrats cleared of litter while litter clearing had little or no effect on native species.

Litter and debris did not seem to limit recruitment of native species in this study. This result is good news for the impact of invasives in rainforest habitats following cyclone disturbance. Invasives appear to be more suppressed by the large input of leaf litter following a cyclone than the native species. None of our plots were located in areas that contained edge habitat (e.g. road or track edges, land-use change edges etc.), however, and the situation around edges may be quite different with potentially lower litter and debris loads, where rainforest patches abut cleared areas for example, coupled with a higher density of invasive species owing to the higher light levels.

The relatively high mortality of invasive herbs and low mortality of invasive shrubs and the invasive tree suggest that while some invasives may comprise a transient component of the native flora, some may go on to have longer-term effects. The *Solanum* shrubs are all highly light-demanding and will likely persist and reproduce as long as the canopy remains relatively open. As light levels decrease over time, the mortality of these species will likely increase. In the mean time however, the effect of the presence of these species is to usurp space, subsequently reducing the rate of recruitment and succession of native species in the understorey. Furthermore, should there be another cyclone or significant disturbance before the canopy recovers these fast-growing and early reproducing shrubs will have the capacity to rapidly spread through the landscape and increase their contribution to the community.

Rubus alceifolius (Giant Bramble) is a fleshy-fruited, shade-intolerant, scrambling shrub capable of smothering other plants and forming dense thickets. Bramble thickets are relatively common in the area around the research site, the largest covering nearly 1500 m^2 with basal diameters up to 150 mm (T. Sydes, pers. comm. 2007). These bramble thickets may have arisen as a result of Cyclone Winifred in 1986. Rapid growth of scrambling species and vines post-cyclone disturbance has been shown to inhibit recruitment of native species, creating the phenomenon of 'strangled gaps' in tropical forests (Horvitz & Koop 2001). Where enough standing trees remain in the study area to allow the canopy to close over in the relatively short term (i.e. 10–15 years), *Rubus* will likely be fairly transient. However, the species may persist for tens to hundreds of years in areas where tree damage has been most severe (e.g. damage score 1.5), consequently retarding the succession response of native species and dramatically altering the structure and composition of the forest in the longer-term.

The invasion of the Wet Tropics rainforests by *M. calvescens* poses a major threat. This species (and other non-native Melastomes) is somewhat shade tolerant and fleshy fruited, and is a serious invader in other tropical places including Hawaii and Tahiti where it has essentially taken over large tracts of rainforest habitat (Meyer 1998a). Invasions of Tahitian rainforests by *M. calvescens* dramatically accelerated after damage caused by cyclones (Merlin & Juvik 1995). *Miconia calvescens* is a declared Class 1 weed in Queensland and the current research site is contained within an area where its active eradication and management is being carried out. In this study, *M. calvescens* has recruited mostly in fully cleared quadrats (11 of 13 recruits). Further monitoring will provide a clearer understanding of its ability to persist and compete with other shade-tolerant native species in the decreasing light levels.

We have previously shown that invasives in rainforest communities are significantly over-represented by shade-intolerant species compared with the native flora and that invasives tend to occupy distinct regeneration niches that are rare or absent in the native vegetation (Murphy *et al.* 2006). It is likely that functional trait differences also exist between natives and invasives in this community that affect their relative ability to disperse to and recolonize disturbed habitat. Ongoing monitoring will elucidate the longer-term impacts of invasive species in rainforest habitats recovering from the cyclone.

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REFERENCES

Baker P. J., Bunyavejchewin S., Oliver C. D. & Ashton P. S. (2005) Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecol. Mono.* **75,** 317–43.

Beach Protection Authority (1986) *Report on Cyclone 'Winifred'*. [Cited 1 December 2007.] Available from URL: http://www.epa.qld.gov.au/publications?id=1881

Bellingham P. J., Tanner E. V. J. & Healy J. R. (2005) Hurricane disturbance accelerates invasion by the alien tree Pittosporum undulatum in Jamaican mountain rain forests. *J. Veg. Sci.* **16,** 675–84.

Bureau of Meteorology (2007) *Severe Tropical Cyclone Larry*. Bureau of Meteorology, Melbourne. [Cited 1 December 2007.] Available from URL: http://www.bom.gov.au/weather/qld/cyclone/tc_larry/Larry_report.pdf

Burslem D. F. R. P. & Whitmore T. C. (1999) Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *J. Veg. Sci.* **10,** 767–76.

Connell J. H., Debski I., Gehring C. A. *et al.* (2005) Dynamics of seedling recruitment in an Australian tropical rainforest. In: *Tropical Rainforests: Past, Present and Future* (eds. E. Bermingham, C.W. Dick, & C. Moritz) pp. 486–506. University of Chicago Press, Chicago and London.

Debski I., Burslem D. F. R. P. & Lamb D. (2000) Ecological processes maintaining differential tree species distributions in an Australian subtropical rain forest: implications for models of species coexistence. *J. Trop. Ecol.* **16,** 387–415.

Denslow J. S. (1987) Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* **18,** 431–51.

Guzmán-Grajales S. M. & Walker L. R. (1991) Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23,** 407–13.

Harms K. E., Wright S. J., Calderon O., Hernandez A. & Herre E. A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404,** 493–5.

doi:10.1111/j.1442-9993.2008.01904.x

Hille Ris Lambers J. & Clark J. S. (2003) Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Can. J. For. Res.* **33,** 783–95.

Hopkins M. S. & Graham A. W. (1987) Gregarious flowering in a lowland tropical rainforest: a possible response to disturbance by Cyclone Winifred. *Aust. J. Ecol* **12,** 25–9.

Horvitz C. C. & Koop A. (2001) Removal of nonnative vines and post-hurricane recruitment in tropical hardwood forests of Florida. *Biotropica* **33,** 268–81.

Horvitz C. C., Pascarella J. B., McMann S., Freedman A. & Hofsetter R. H. (1998) Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecol. Appl.* **8,** 947–74.

Hubbell S. P., Foster R. B., O'Brien S. T. *et al.* (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283,** 554–7.

Knutson T. R. & Tuleya R. E. (2004) Impact of CO2-induced warming on simulated hurricane intensity and precipitation: sensitivity to the choice of climate model and convective parameterization. *J. Clim.* **17,** 3477–95.

Merlin M. D. & Juvik J. O. (1995) Montane cloud forests in the Tropical Pacific: some aspects of their floristics, biogeography, ecology and conservation. In: *Tropical Montane Cloud Forest* (eds L. S. Hamilton, J. O. Juvik & F. N. Scatena) pp. 234–53. Springer-Verlag, New York.

Metcalfe D. J., Bradford M. G. & Ford A. J. (2008) Cyclone damage to tropical rain forests: species- and community-level impacts. *Aust. Ecol.* **33,** 432–41.

Metcalfe D. J. & Ford A. J. (2007) *Floristic Biodiversity in the Wet Tropics*. In: *Living in a Dynamic Tropical Forest Landscape* (eds N. Stork & S. Turton) pp. 123–32. Blackwell, Oxford (in press).

Metcalfe D. J. & Turner I. M. (1998) Soil seed bank from lowland rain forest in Singapore: canopy-gap and litter-gap demanders. *J. Trop. Ecol.* **14,** 103–8.

Meyer, J-Y. (1998a) Epidemiology of the invasion by *Miconia calvescens* and reasons for a spectacular success. In: *Proceedings of the First Regional Conference on* M. calvescens *Control* (eds J.Y. Meyer and C.W. Smith) pp. 72–7. Papeete, Tahiti, French Polynesia.

Murphy H. T., Westcott D. A. & Metcalfe D. J. (2006) Functional diversity of native and invasive plant species in tropical rainforests. In: *Proceedings of the 15th Australian Weeds Conference* (eds C. Preston, J. H. Watts, N. D. Crossman) pp. 199–202. Weed Management Society of South Australia, Adelaide.

Queensland Government Environmental Protection Agency (2006) *Regional Ecosystem Framework*. [Cited 1 December 2007.] http://www.epa.qld.gov.au/projects/redd/display_region.cgi?region=7&format=print

Tanner E. V. J. & Bellingham P. J. (2006) Less diverse forest is more resistant to hurricane disturbance: evidence from montane rain forests in Jamaica. *J. Ecol.* **94,** 1003–10.

Turton S. M. (2008) Landscape-scale impacts of Cyclone Larry on the forests of northeast Australia including comparisons with previous cyclones impacting the region between 1858 and 2006. *Austral Ecol.* **33,** 409–16.

Turton S. M. & Stork N. E. (2008) Impacts of tropical cyclones on forests in the wet tropics of Australia. In: *Living in a Dynamic Tropical Forest Landscape* (eds N. E. Stork & S. M. Turton) pp. 47–58. Blackwell, Oxford (in press).

Unwin G. L., Applegate G. B., Stocker G. C. & Nicholson D. I. (1988) Initial effects of tropical cyclone 'Winifred' on forests in north Queensland. *Proc. Ecol. Soc. Aust.* **15,** 283–96.

Uriarte M., Canham C. D., Thompson J., Zimmerman J. K. & Brokaw N. (2005) Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *J. Ecol.* **93,** 291–304.

Walker L. R. & Neris L. E. (1993) Post hurricane seed rain dynamics in Puerto-Rico. *Biotropica* **25,** 408–18.

Walker L. R., Lodge S. J., Guzmán-Grajales S. M. & Fetcher N. (2003) Species-specific seedling responses to hurricane disturbance in a Puerto Rican rain forest. *Biotropica* **35,** 472–85.

Webster P. J., Holland G. J., Curry J. A. & Chang H. R. (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* **309,** 1844–6.

Yamashita N., Ishida A., Kushima H. & Tanaka N. (2000) Acclimation to sudden increase in light favouring an invasive over native trees in subtropical islands, Japan. *Oecologia* **125,** 412–9.

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