Spatial and temporal patterns of exotic species recruitment in a cyclone-damaged tropical forest

Helen T. Murphy, Matt G. Bradford, Andrew J. Ford and Daniel J. Metcalfe
CSIRO Ecosystem Sciences and CSIRO National Climate Adaptation Flagship, PO Box 780, Atherton, Qld 4883, Australia
Corresponding author: Helen.Murphy@csiro.au

Summary Cyclones are relatively infrequent, cause massive and widespread disturbance to tropical regions and are recognised as important structuring events in tropical forest communities. Extensive defoliation, loss of major branches and multiple treefalls result in a significantly more open canopy providing ideal conditions for establishment and rapid spread of exotic species. Understanding the long-term implications of these major disturbances on invasion, and subsequently on tropical forest composition and structure will be vital to understand likely future changes to native species distributions, community structure and ecosystem function. Severe Tropical Cyclone Larry (category 4) crossed the North Queensland coast of Australia on Monday 20 March 2006. Over the past 3½ years we have monitored recruitment, growth and mortality of all native and exotic species in an area damaged by the cyclone. We report here on patterns of exotic species recruitment across a damage gradient, and with manipulation of litter and debris loads. We discuss the implications of our results for weed management post-cyclone and highlight potential impacts on native species diversity.

Keywords Cyclone, hurricane, diversity, recruitment, rainforest.

INTRODUCTION

The widespread and severe disturbance caused by cyclones provides ideal conditions for rapid recruitment and spread of some exotic plant 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 in tropical forests (Bellingham *et al.* 2005). For example, the rapid invasion of the small tree *Miconia calvescens* DC. in Tahiti is often attributed to the six hurricanes that hit the Society Islands between December 1982 and April 1983. Birnbaum (1991, 1994, cited in Meyer 1998) reported that the cyclones explained the 'demographic explosion of *Miconia*', and that 'the speed of the invasion then became astonishing'.

In the Wet Tropics of Australia, it is likely that cyclones have always been important structuring events in rainforest communities. However, the compounded effects of an increasing number and diversity of exotic species in tropical habitats, and the possibility of an increasing intensity of cyclones as a result of changing climatic conditions (Emanuel 2005) may result in significant and relatively rapid changes to forest composition, diversity and structure.

Severe Tropical Cyclone Larry 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 and beyond. Over the past 3½ years we have monitored recruitment, growth and mortality of all native and invasive species in an area severely damaged by the cyclone. Twelve months after the cyclone passed, we analysed the short-term recruitment dynamics of native and invasive species and suggested that invasive species would be mostly transient with a smaller proportion of species likely to be persistent (Murphy *et al.* 2008a).

Here we examine nearly 4 years of monitoring data to determine the patterns of exotic species recruitment over the medium-term and discuss the implications for weed management. We also highlight the potential impacts of weed invasion post-cyclone on native species succession and diversity.

MATERIALS AND METHODS

The study site is located 1 km west of the township of El Arish, in North Queensland (17°48S, 145°59E) (Figure 1). The site is partly located on private property and extends into Japoon National Park and the Wet Tropics World Heritage Area. The eye of the cyclone crossed the coast approximately 25 km north of the site. Maximum wind gusts experienced at the site were likely to be up to 240 km h^{-1}. The entire area in which the study site was established was damaged by Cyclone Larry although damage varied substantially over relatively small scales, depending particularly on aspect (H. Murphy personal observations).

Eleven 50 × 20 m plots were established in the study area in areas ranging from severely damaged with multi-directional impact and extensive tree damage, to areas characterised mostly by massive

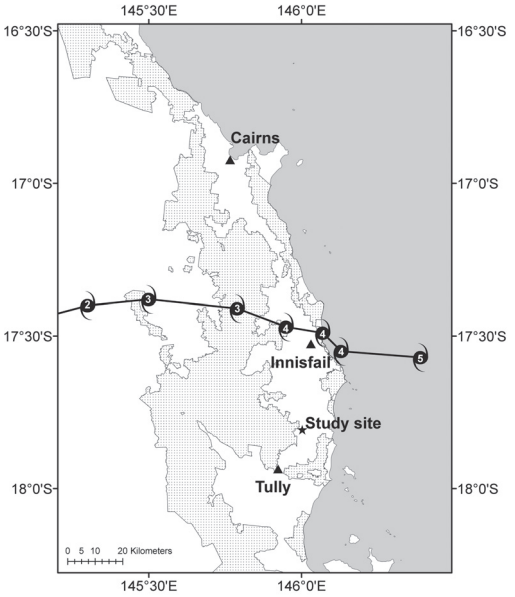

Figure 1. Location of the study site and the track taken by Cyclone Larry. Numbers within the cyclone symbol indicate the category of the cyclone. The Wet Tropics World Heritage Area is shaded grey.

defoliation. The damage level of each plot was scored on the Bradford-Unwin damage scale (Metcalfe *et al.* 2008). On this scale plots were located in damage level 1.5 – 'severe and common disturbance' (6 plots); 2 – 'severe and localised 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 99 quadrats). Three quadrats were assigned to each of three litter treatments: (1) uncleared, i.e. no treatment, (2) partially cleared, with coarse woody debris removed (i.e. all woody debris with diameter >2 cm), and (3) fully cleared of leaf litter and debris down to the soil layer.

All angiosperms and gymnosperms in each quadrat were labelled with a numbered aluminium tag. 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. All newly emerged seedlings were tagged, identified and the height estimated at each survey. Leaf litter and debris were removed from fully cleared quadrats (treatment 3), and woody debris from partially cleared quadrats (treatment 2) at each survey period. Monitoring was undertaken every 3–4 months initially and in the last year, every 6 months. Results reported here are for the first eleven surveys in the 3½ years following the cyclone, i.e. initial set-up (first survey) (T1), second survey (T2), etc., through to eleventh survey (T11).

RESULTS

In the 3½ years since the cyclone we recorded recruitment of a total of 2243 individuals from 14 exotic species. The entire database (i.e. natives and exotics) consisted of 19,477 individuals from approximately 289 species (4% of individuals in the database could only be indentified to genus), 187 genera, and 79 families. Thus, exotics made up nearly 12% of all recruits.

Two peaks of exotic species recruitment occurred; one in the first summer (06/07) following the cyclone and one in the second summer (07/08) (Figure 2a).

The recruitment peaks were almost entirely driven by herbaceous species (including *Ageratum conyzoides* L., *Crassocephalum crepidioides* (Benth.) S.Moore and *Erechtites valerianifolius* (Wolf) DC.) (Figure 2b). Woody exotics (including *Rubus alceifolius* Poir., *Miconia calvescens* and *Solanum* spp.) occurred in much lower numbers but were persistent throughout the time frame of the study, with low mortality rates.

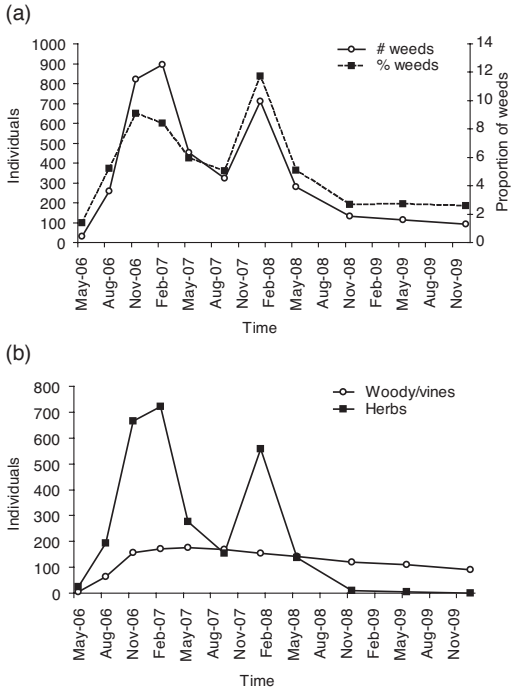

Figure 2. Exotic species abundance over time since the cyclone for (a) all species combined and (b) for herbaceous and woody exotics separately.

Exotic species were more abundant in the most severely damage quadrats (Figure 3a) and in the quadrats that were fully cleared of all litter and debris (Figure 3b).

DISCUSSION

The results of this analysis confirm our initial speculation (Murphy *et al.* 2008a) about the transient nature of most of the exotic flora in rainforest habitats following a severe cyclone. However, the second peak of exotic species recruitment, which was of a similar magnitude to the first peak, indicates that any impacts of weeds on native species succession are likely to extend up to 2 years post-disturbance, particularly in the most severely disturbed areas. The peak of exotic species recruitment in the second summer was not reflected in the patterns of native species recruitment; the rate of native species recruitment declined steadily from the first summer peak after the cyclone, and has generally reached a plateau in the most recent year. By the third year, light levels reaching the forest floor had been very much reduced due primarily to resprouting of existing live shrubs and trees as well as rapid growth of native recruiting pioneers. Our results indicate that by this time conditions are no longer suitable for exotic species recruitment, although established species may persist. Bellingham *et al.* (1996) also found after Hurricane Gilbert in Jamaica that light levels at 1 m above the forest floor returned to pre-hurricane levels within 33 months.

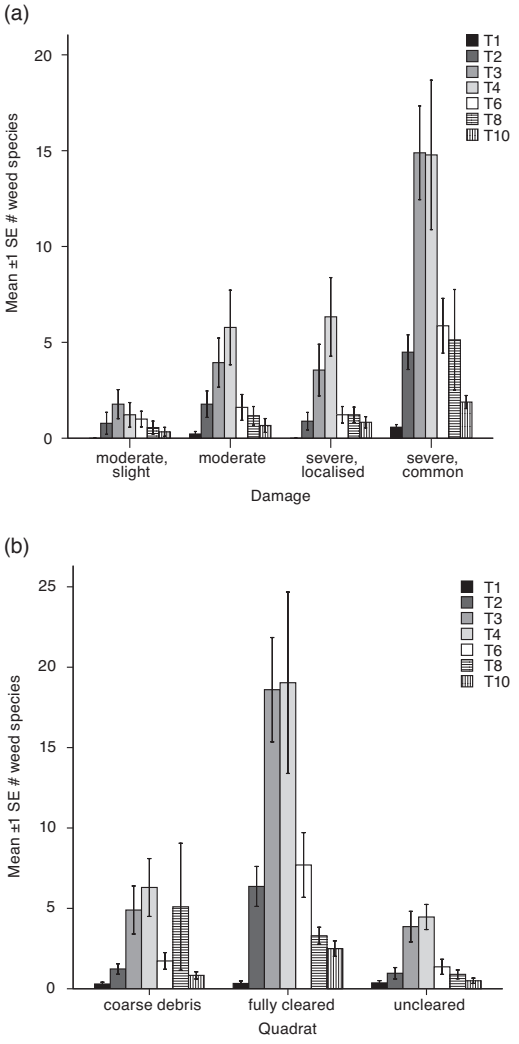

Figure 3. Number of (±1 SE) weed species with (a) damage level and (b) quadrat treatment over time from initial set-up (T1) to T4, and T6, T8 and T10. Not all monitoring events are shown for clarity.

While it appears the most severe cyclone damage conditions are ideal for exotic species recruitment, the very high litter and debris loads present a significant barrier to establishment. Based on the mean number of exotics at each time period in the uncleared quadrats (across all damage levels), if all quadrats had been uncleared, exotics may have made up as little as 7% of the total individuals in the entire species pool (as opposed to 12%). The obvious implication for weed management post-cyclone is that while herbaceous exotic species appear abundant and widespread initially, most are transient. In comparison, woody exotics, which are less obvious initially, are relatively persistent, and this is where management effort should be focused.

The most abundant woody exotic at the site is the scrambling shrub, *Rubus alceifolius*, or giant bramble (215 individuals). 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 and Koop 2001). Less abundant but of concern is the small woody tree, *Miconia calvescens* (20 individuals); this species is fleshy-fruited, shade tolerant and is considered one of the worst invasive weeds across the Pacific. We have already shown a rapid response in growth rates of existing *M. calvescens* plants at the site to the opening of the canopy caused by the cyclone (Murphy *et al.* 2008b). The *M. calvescens* post-cyclone recruits continue to show low mortality and the species is persisting in the now almost completely shaded understorey as seedlings. *M. calvescens* is currently an eradication target in Australia, and outside of the study plots it is regularly

controlled in the surrounding area. Our results are consistent with research and anecdotal information from other Pacific Islands such as Hawaii and Tahiti (Meyer 1998, Murphy *et al.* 2008b) that indicate the importance of cyclones in the invasion success of *M. calvescens* and the imperative nature of a long-term eradication effort.

Woody exotics tend to play a similar functional role to native pioneer species in tropical rainforest communities (Murphy *et al.* 2006). Native pioneer species also are more abundant in the most severely damaged quadrats surveyed (Murphy *et al.* 2008a). Our data suggest that their ongoing presence in the community is maintained to a large degree by relatively rare, large-scale and severe disturbances such as cyclones. Native pioneers play a vital role following such disturbances, contributing to the rapid development of shade and facilitating recruitment of later-successional species (Walker *et al.* 2010). While native pioneer species make up a relatively small component (*c.* 15–18%) of the native regional species pool at this site (H. Murphy unpublished data), the total number of woody weed species we have recorded at the site is six. Replacement of native pioneers by woody weeds that fill a similar functional role will lead to reductions in diversity because replacement is likely to be on a one-for-many basis. Invasion tends to homogenise communities over large scales because invasive species are typically widespread and commonly shared across communities (Olden 2006). Tropical forests have traditionally been seen as particularly resistant to invasion because they have high native species diversity and more fully utilise all available niche space compared with, for example, temperate forests (Fine 2000). A reduction in diversity of native pioneer species and an increase in homogenisation may have the effect of decreasing resistance to invasion in cyclone damaged forest in the future.

ACKNOWLEDGMENTS

This work has been funded by the Weeds CRC, Biosecurity Queensland, the Australian Weeds Research Centre and the Marine and Tropical Sciences Research Facility. We are grateful to David Chandlee and Queensland Parks and Wildlife for permitting us to work on their land.

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