Journal of Vegetation Science **27** (2016) 133–143

Dynamic response of a Philippine dipterocarp forest to typhoon disturbance

Sandra L. Yap, Stuart J. Davies & Richard Condit

Keywords
Biomass; Dipterocarp forest; Forest dynamics; Forest resilience; Mortality and recruitment; Regeneration; Tree demography; Typhoon disturbance

Nomenclature
Co et al. (2006)

Received 5 August 2014
Accepted 5 February 2015
Co-ordinating Editor: Kerry Woods

Yap, S.L. (slimyap@gmail.com)[1],
Davies, S.J. (corresponding author, DaviesS@si.edu)[2],
Condit, R. (conditr@gmail.com)[3]

[1]Institute of Biology, University of the Philippines, Diliman, Quezon City, PH 1101, Philippines;
[2]Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, PO Box 37012, Washington, DC 20013-7012, USA;
[3]Smithsonian Tropical Research Institute, PO Box 0843-03092, Balboa, Ancon, Panama

Abstract

Questions: Natural hazards can wreak catastrophic damage to forest ecosystems. Here, the effects of typhoon disturbance on forest structure and demography of the 16-ha Palanan Forest Dynamics Plot in the northeast Philippines were examined by comparing census intervals with (1998–2004) and without (2004–2010) a strong typhoon. Category 4 Typhoon Imbudo, with wind gusts exceeding 210 kph, hit Palanan in July 2003. In this study, we ask: (1) was there an effect of the typhoon on stand structure and biomass; (2) was there an impact on species diversity; (3) did annual mortality, growth and recruitment change significantly between typhoon and non-typhoon periods; and (4) did the typhoon's impact vary with local topography, from leeward to windward sides of a ridge?

Location: Lowland mixed dipterocarp forest, Palanan, Isabela, Philippines.

Methods: Census data from 1998, 2004 and 2010 for all trees $\geq$1 cm DBH in a 16-ha permanent plot in Palanan, Isabela, were used to assess tree demography. Recorded in the census were species identification and measurements of DBH and tree locations. Biomass was calculated from published allometry.

Results: Species diversity and stand structure remained stable, except for an increase in small-sized trees (1–2 cm) recorded in the census conducted within a year of the typhoon disturbance. Tree mortality was significantly higher during the typhoon interval at $2.27\%\cdot\text{yr}^{-1}$ and more so in windward than leeward habitats. Above-ground biomass loss in the typhoon interval was minimal (2.64%) and biomass exceeded pre-typhoon levels after 6 yrs. Recruitment rate during the typhoon interval was almost four times the rate in the non-typhoon interval that followed, attributed to the rapid growth of seeds and seedlings of pioneer species due to the open, defoliated canopy. Negative population growth was recorded for the early successional species in the non-typhoon interval. Significantly higher growth rates of trees in the non-typhoon interval also contributed to biomass gain.

Conclusions: Mortality, recruitment and growth rates vary across a heterogeneous landscape and are related to typhoon disturbances. The relatively low mortality and fast recovery of the Palanan forest demonstrates the resistance and resilience of the forest to intense episodic typhoon disturbances.

Introduction

Typhoons and hurricanes are among the most severe natural disturbances forests ever face, leading Yih et al. (1991) to conclude that "the appropriate metaphor for natural ecosystems is not eternal constancy, but rather cycles of death and resurrection" after studying Hurricane Joan in Nicaragua. In New England, 70% of trees were felled during a 1938 hurricane (Foster 1988), while in Nicaragua, Hurricane Joan damaged 75% of trees in the rain forests it struck (Boucher et al. 1990). Most such studies on the impact of tropical storms have been done in the Americas, particularly in Puerto Rico, where major hurricanes pass every 50–60 yrs (Zimmerman et al. 1994; Ostertag et al. 2005). In the tropical western Pacific, typhoons recur much more frequently: category-five storms, with winds

Doi: 10.1111/jvs.12358

>250 kph, pass over Fushan Forest in Taiwan every 12 yrs on average (Mabry et al. 1998), and in the northeast Philippines, three category-five storms struck in the last 10 yrs. Yet few studies of typhoon damage on forests have been done in Asia (Lin et al. 2011), and none in the Philippines. This begs the question of how typhoons impact Asian forests: could 70% of the trees in a Philippine forest be toppled every decade?

Dense and tall dipterocarp forests dominate the landscape throughout the Malesian region (Maury-Lechon & Curtet 1998). In the Philippines, these forests are special because local endemism is high. Philippine forests harbour >9000 plant species, 50% of which are endemic (Merrill 1926; Myers et al. 2000). Unfortunately, only 7% of the old-growth closed-canopy forests remain (Heaney & Regalado 1998). Severe damage to these remnants during typhoons could thus put species at risk of extinction. In order to quantify typhoon damage, we established a permanent plot in the Palanan forest of northeast Luzon Island in 1994. With a powerful typhoon in 2003, we now have complete censuses of 100 000 trees during a typhoon-impacted interval (1998–2004) and a non-typhoon interval (2004–2010), providing a comparative measure of typhoon impact on forest dynamics. We investigated the effects of typhoon disturbance on: (1) stand structure, species diversity and biomass; (2) annual mortality, growth and recruitment; and (3) both of these in relation to the varying topography from leeward to windward sides of a ridge. We predicted that the typhoon disturbance would result in lower tree density across all diameter classes, reduced species diversity and reduced biomass. We also expected that annual mortality would be higher in the typhoon interval, with growth and recruitment rates higher in the non-typhoon interval that followed. Moreover, we anticipated increasing impacts from leeward to windward habitat types.

Methods

Study site

The research was conducted in a mixed dipterocarp forest of the Northern Sierra Madre Natural Park in Isabela, Philippines, on the northeast coast of Luzon Island, in the foothills of the Sierra Madre Mountains (Fig. 1). The area is characterized by an ever-wet climate with mean annual rainfall of 3218 mm, with individual years ranging from 1347 to 6841 mm (Co et al. 2006). From Nov to Jun, northeast winds off the Pacific bring rain to the eastern side of the Sierra Madre, and during the other half of the year, tropical cyclones approach from the southeast. Between 1948 and 2004, nine typhoons made landfall in the Philippines per year (pagasa.dost.gov.ph). Among the many that

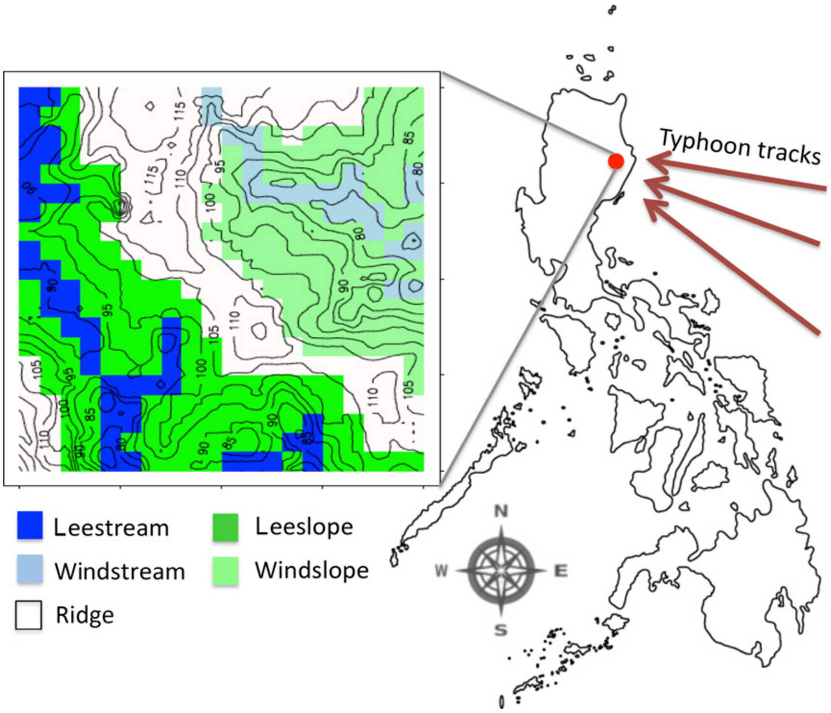

Fig. 1. Map of the 16-ha Palanan FDP showing its topography, habitats and position along typhoon tracks. The Palanan FDP is located in the Pacific coast of Luzon Island exposed to the direction of most typhoons. The five habitat types represented are leestream, windstream, ridge, leeslope and windslope.

visited the area, Category-four Typhoon Imbudo (local name: Harurot) hit the Pacific coast of northeast Luzon on 22 July 2003, with maximum sustained winds of 210 kph (pagasa.dost.gov.ph). It was reported by local communities to have inflicted extensive damage in and around Palanan, Isabela.

The tree census

A permanent, 16-ha forest census plot was established at 17°02′36 N, 122°22′58 E in 1994 and named the Palanan Forest Dynamics Plot (Co et al. 2006). The Palanan Plot is a member of the network of long-term plots of the Center for Tropical Forest Science (CTFS, www.ctfs.si.edu), and plot establishment followed the standard CTFS protocol (Condit 1998). Work began in 1994, when 8 ha of forest were censused; in 1998, the plot was extended to 16 ha. Re-censuses of the 16 ha were completed in 2004 and 2010. At each census, all trees ≥1 cm DBH were tagged, measured, mapped and identified to species. Here we report on the three full censuses of 16 ha, providing estimates of forest demography and change over 1998–2004 and 2004–2010. With Typhoon Imbudo passing over the plot in July 2003, the former interval included the typhoon impact while the latter did not. The census of 2004 began in Dec 2003, and was finished by Jun 2004, within 12 months of Imbudo passing over.

Plot topography

Geodetic engineers from L.A.P. Surveying of Tuguegarao City, Cagayan, performed the topographic survey of the Palanan plot in Aug 2000. Elevation within the 16-ha plot ranges from 77 to 118 m a.s.l. Topographic features of the plot include a ridge diagonally crossing the plot in a northwest direction and a stream along each side of the ridge (Fig. 1). In order to assess whether forest dynamics were affected by topography, we divided the plot's 400 20 m × 20 m quadrats into five categories based on elevation, aspect and location of streams (Fig. 1, Table 1). The ridge habitat includes quadrats above the 70th percentile of the elevation range (≥104.4 m). East of the ridge is the windward side directly facing incoming typhoons, and west of the ridge the leeward, unexposed side. Directly adjacent to ridge habitats, on both windward and leeward sides, are quadrats sloping down to the streams bisecting the plot, ranging from <104.4 m a.s.l. to 77 m a.s.l. (26-m range), correspondingly referred to as windslope and leeslope habitats. Similarly, streamside quadrats are referred to as windstream and leestream habitats on the east and west of the ridge, respectively. Streams are recognized as distinct habitats as other studies have shown species–habitat associations with streamside niches (Harms et al. 2001; Chuyong et al. 2011).

Taxonomy

Every individual not identified immediately in the field by an experienced botanist (James V. LaFrankie or Leonard L. Co) had leaves with or without flowers collected. The unknown specimens were sorted into groups thought to be single species, then compared to specimens at the University of the Philippines Herbarium (PUH), Philippine National Herbarium (PNH) and Harvard University Herbarium (HUH). Herbarium vouchers for each morphospecies are currently stored at the PUH and Isabela State University. Those still not identified were given morphospecies names, and demographic rates of those morphospecies were calculated just as for the rest of the species whose identity is known. Some individuals could not be assigned to any species group; these unknowns were included in stand-wide demographic estimates, but not in estimates of individual species. In the 2010 census, there were 75 335 individual trees alive: 92.7% belonged to 278 fully identified species, 7.2% belonged to 37 morphospecies (known to genus) and 0.08% remained unidentified.

Mortality

Annual mortality rate was calculated as $(\log N_1 - \log S_2)/T$, where N_1 is the number of individuals alive in census 1, S_2 the number of individuals surviving at census 2, and T the time interval (yrs) between censuses (Condit et al. 1999). Mortality was calculated for diameter categories by subsetting trees based on their initial diameter, topographic

Table 1. Quadrat assignments into five habitat categories according to elevation, aspect and stream location.

Habitat Type	Topographic Feature			Area (No. of Quadrats, ha.)
	Elevation, m	Aspect	Stream	
Ridge	≥104.4	Ridge	Non-streamside	114, 4.56
Leeslope	<104.4	Leeward	Non-streamside	120, 4.80
Leestream	<104.4	Leeward	Streamside	42, 1.68
Windslope	<104.4	Windward	Non-streamside	102, 4.08
Windstream	<104.4	Windward	Streamside	22, 0.88

habitat categories and species. Note that cause of tree death was not recorded.

Growth

Annual growth was defined as the diameter increment, $(dbh_2 - dbh_1)/T$, for each individual tree, discarding cases where the stem broke as well as outliers that must have been erroneous measurements (Condit et al. 2004). As for mortality, mean growth rates were estimated for separate diameter categories and topographic regions.

Recruitment

Recruitment was defined as the rate at which new 1-cm stems entered the census, computed as $(\log N_2 - \log S_2)/T$, where N_2 is the total number of individuals alive and ≥1 cm DBH in census 2 and S_2 the survivors in census 2 (Condit et al. 1999). Recruitment was calculated separately for the five habitats.

Biomass

Above-ground biomass for individual trees was obtained using the regression model in Chave et al. (2005) for moist forests; since we did not measure tree height, we used the Chave et al. equation that omits the height term. Wood density for individual species was taken from the table published in Chave et al. (2009). For 102 species found in the Palanan plot, Chave et al. (2009) included a record. For 189 species, a genus-wide mean was utilized because Chave et al. did not include the species found in the Palanan plot; for 30, a family-wide mean was used.

Diversity and stand structure

Species richness per census and habitat was found by tallying living stems. Fisher's α was used as the measure of species diversity. Stand structure is the distribution of age classes in the tree community, represented here by the frequency distribution of size (DBH) classes.

Statistical analysis

Our null hypothesis regarding changes in demographic rates and species diversity was that the typhoon and non-typhoon intervals would not be different. To test this, 95% confidence limits were generated for every statistic. For mortality and recruitment, which are based on proportions of individuals, confidence limits are provided by the β-distribution. For growth rates, confidence intervals were calculated using standard t-statistics. Validity of these tests has been confirmed elsewhere (Condit et al. 1999, 2004). For all these demographic estimates, the CTFS R Package provides software for calculations. The Vegan package in R (R Foundation for Statistical Computing, Vienna, AT) provided confidence limits for Fisher's α. In the case of total forest above-ground biomass, we only report a single sum across 16 ha, with no confidence intervals since there are no replicates at this scale. All analyses were carried out with RStudio v.0.98.978 (RStudio Inc., Boston, MA, USA).

Results

Immediate impact

We visited the Palanan Plot 3 weeks after Typhoon Imbudo passed. On the ridge-top and east-facing windward slopes, defoliation was near complete, but the leeward side was visually less damaged (Fig. 2a,b). Sprouting and subsequent re-foliation was noticeable within 3 months following the typhoon and a closed canopy was observed within 12 months (S.L. Yap, pers. obs.).

Species diversity and forest structure

In 1998, there were 309 tree species with a DBH ≥ 1 cm in the 16-ha plot. This increased slightly to 317 in 2004 then

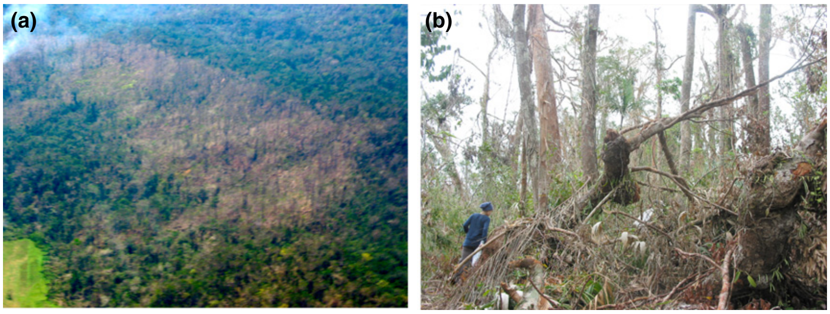

Fig. 2. Images of defoliation and disturbance in the Palanan FDP. Defoliation in the windward side of the hill-ridge where the Palanan plot is located as seen flying in from the northwest direction (**a**), and as seen from the ridge inside the plot (**b**).

Doi: 10.1111/jvs.12358

315 in 2010. Species diversity, measured by Fisher's α, did not vary significantly among censuses (Table 2).

The number of trees increased by 22% from 1998 to 2004, the typhoon interval, then fell back slightly over the next interval, but was still 17% higher in 2010 than in 1998 (Table 2). The increase in density was nearly all due to an increase in small trees (1–2 cm DBH), with little change in mid- to large-diameter trees (Fig. 3a).

Table 2. Changes in diversity and stand structure in the MDF of Palanan.

	Census Populations		
	1998	2004	2010
Taxa	309	317	315
Individuals	64 217	78 096	75 335
Fisher's α	42.16	42.12	42.05
Basal Area (m^{2}·ha^{-1})	38.95	38.43	42.28
Biomass Stock (t·ha^{-1})	409.66	398.83	444.6

Mortality and growth

Mortality rate calculated for the whole plot was significantly higher during the census interval that included the typhoon ($2.27 \pm 0.05\%\cdot yr^{-1}$) than during the non-typhoon interval ($2.05 \pm 0.03\%\cdot yr^{-1}$). In small (1–3 cm) and large (≥30 cm) size classes mortality rates were significantly higher during the typhoon interval (Fig. 3b). In contrast, mid-sized trees (4–29 cm) showed no significant difference in mortality rates between typhoon and non-typhoon intervals. Indeed, from 5–15 cm, trees had slightly lower mortality during the typhoon interval than afterward (Fig. 3b).

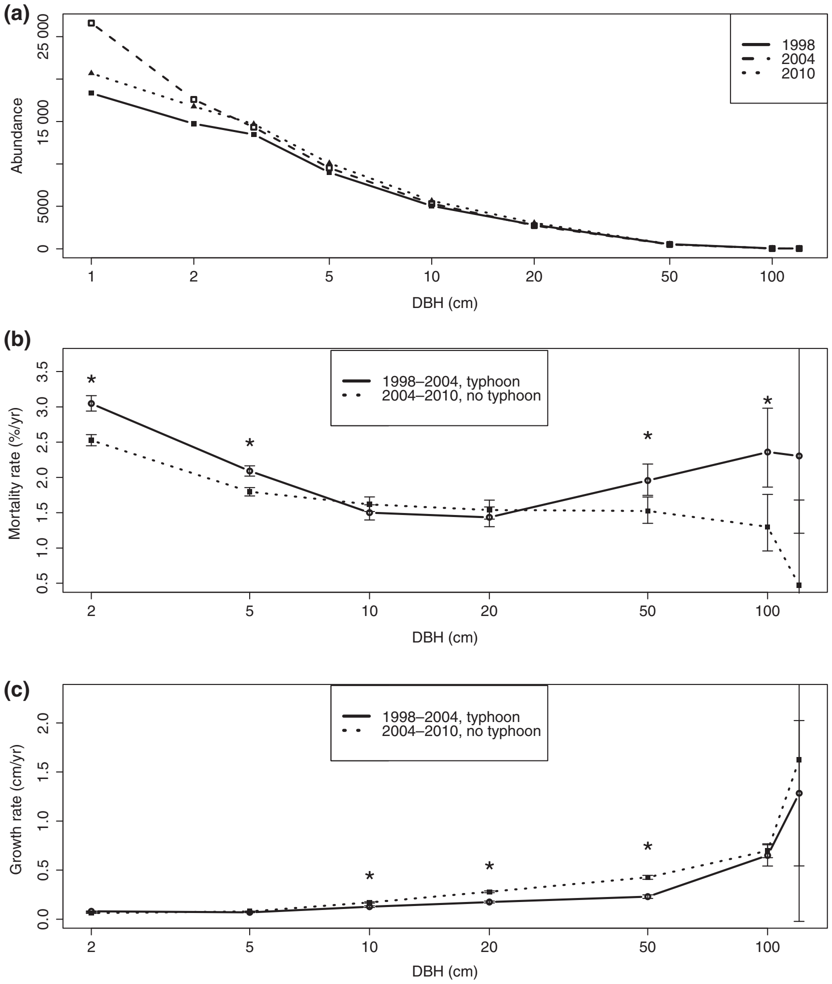

Fig. 3. Changes in forest stand structure and dynamics among size classes over 12 years in the Palanan forest. (**a**) Stand size structure for three plot censuses, and (**b**) mortality and (**c**) growth rates for the typhoon (1998–2004) and non-typhoon (2004–2010) intervals. Mortality and growth rates have 95% confidence limits. Significant differences for specific size classes are denoted with asterisks.

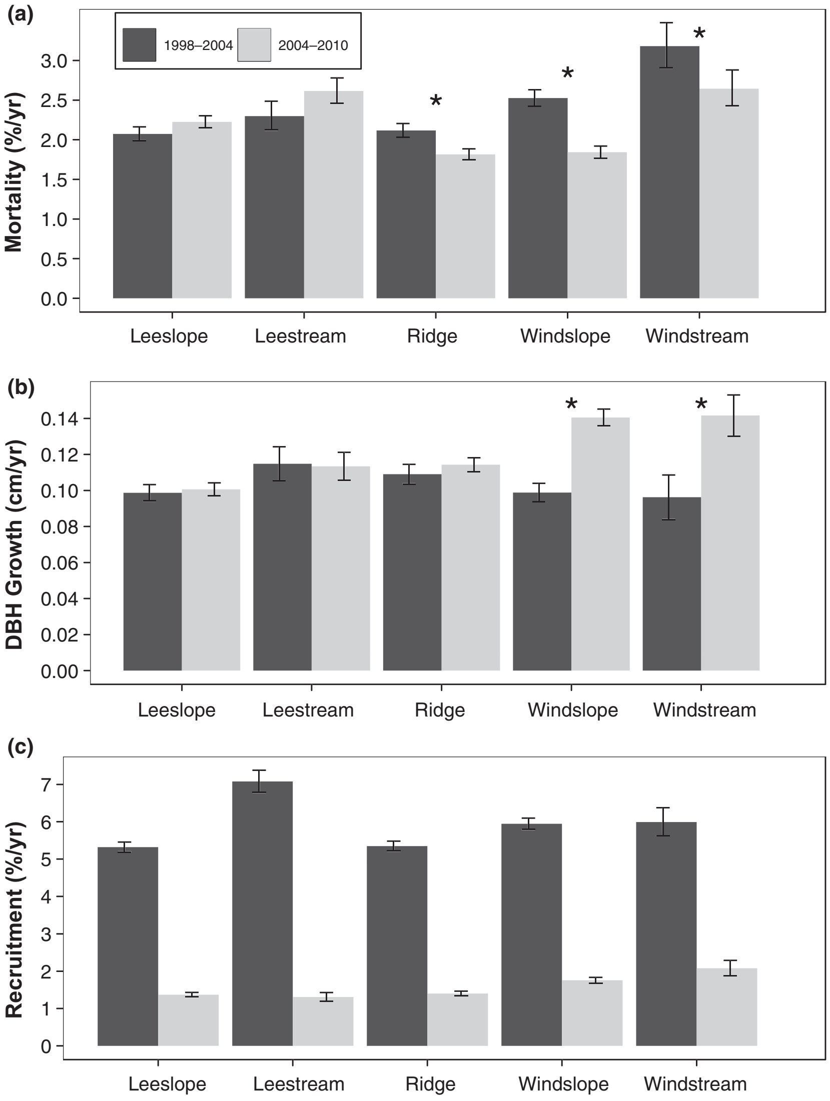

Fig. 4. Variation in demographic rates among habitat types for the typhoon (1998–2004) and non-typhoon (2004–2010) intervals. (**a**) mortality (%·yr^{-1}), (**b**) diameter growth (cm·yr^{-1}), and (**c**) sapling recruitment (%·yr^{-1}). Significant differences between census intervals are denoted with asterisks, except in C where all effects were significant.

Growth rates among trees across the plot were higher in the non-typhoon interval than the typhoon interval. The difference was significant for mid-sized trees, 5–40 cm DBH, but the pattern held for larger trees as well (Fig. 3c).

Among habitats, tree mortality varied in both intervals (Fig. 4a). In the windward and ridge habitats mortality was significantly higher in the typhoon interval. In the leeward habitats, mortality was lower in the typhoon interval but not significantly so from the non-typhoon interval. On the other hand, growth rates did not vary significantly among the five habitats during the typhoon interval, but in the non-typhoon interval there were significant habitat-related differences in growth with increasing growth rates from leeward to ridge to windward habitats (Fig. 4b).

Recruitment

Sapling recruitment varied significantly between typhoon and non-typhoon census intervals (Fig. 4c). Almost 22 000 trees recruited in 2004, while only 6887 trees recruited in 2010. In comparison, the numbers of recruits from 1994 to 1998, a non-typhoon interval, were 4600 trees. In all five habitats, recruitment was three to four times higher during the typhoon interval than the non-typhoon interval. Windward habitats had significantly higher recruitment than leeward and ridge habitats in both intervals except in leestream habitats during the typhoon interval.

The high rate of recruitment in the typhoon interval resulted in increased abundance of most species (Fig. 5a).

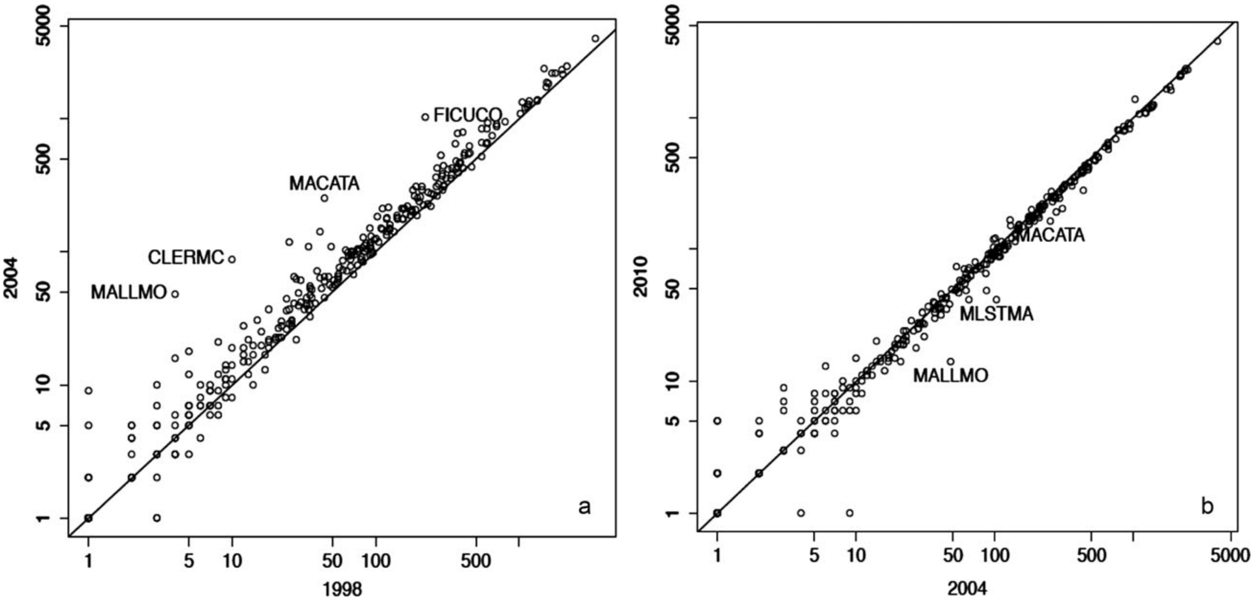

Fig. 5. Differences in species abundances between 1998 and 2004 (a), and 2004 and 2010 (b). Species codes are: CLERMC, *Clerodendrum macrostegium*; FICUCO, *Ficus congesta*; MACATA, *Macaranga tanarius*; MALLMO, *Mallotus mollissimus*; MLSTMA, *Melastoma malabathricum*.

In the non-typhoon impacted interval, most species abundances changed little. However, several species had big increases followed by big declines in abundance in the typhoon and non-typhoon intervals, respectively. These species were well-known gap-demanding species, including *Clerodendrum macrostegium* Schauer, *Macaranga tanarius* (L.) Mull. Arg. and *Mallotus mollissimus* (Geiseler) Airy Shaw (Fig. 5b).

Biomass

The dynamics of mortality, growth and recruitment in the plot among censuses resulted in a small decline in biomass following the typhoon, from 409.7 t·ha^{-1} in 1998 to 398.8 t·ha^{-1} in 2004. Subsequently, biomass increased much more, and by 2010 there was 444.6 t·ha^{-1} in 2010, an 8.5% increase since 1998 (Table 2).

Discussion

The Palanan forest is a diverse lowland tropical rain forest frequently disturbed by strong typhoons. Our study of one site soon after the high-intensity Typhoon Imbudo passed, in comparison to a census interval without a strong typhoon, reveals details of the forest response. To interpret the response, it is important to reiterate the exact timing of censuses: we initiated the 2004 plot census 6 months after the typhoon passed, and finished after another 6 months, just a year after Imbudo. This timing allowed us to detect the mortality impact of the storm, while it also left a post-typhoon window of time during which elevated recruitment could be detected. Typhoon-driven effects are inferred from statistically significant differences with background demographic rates in the non-typhoon interval.

The sequence of events was, we hypothesize, an immediate defoliation of the canopy trees, and an increase in tree mortality and consequent biomass loss, at the time of the typhoon. This opened the canopy, letting light reach lower levels, and the subsequent response was high sapling recruitment and a shift in the composition of the community favouring light-demanding species. Given the timing of the census, we infer that elevated recruitment happened within the first year post-typhoon. By the 2010 census, recruitment had fallen dramatically. Growth rates, however, were higher in the 2004–2010 interval than during 1998–2004. We infer from this that the extra light reaching the post-typhoon forest continued for another year or two after 2004. Thus, storm survivors benefitted from additional light for about half a year of the first interval, but for two or more years of the second interval. The increases in growth quickly restored standing biomass, indeed, there was more in 2010 than in 1998. This certainly indicates resilience of the Palanan forest to severe storm disturbance.

Species diversity and stand structure

A forest that experiences frequent intense disturbances must have species that are adapted to those events. If that is the case, long-term stability in species composition and forest structure may be expected for typhoon-frequented forests. In Palanan, this appears to be true as species diversity showed no significant difference between the typhoon and the non-typhoon intervals. Vandermeer et al. (2000) recorded an increase in species richness in Nicaraguan forests over the 10 yrs following Hurricane Joan. Even after the intense typhoon at Palanan, stand structure was maintained with only a short-term pulse of higher recruitment in 1–2 cm DBH trees.

Mortality and biomass

Increased mortality rates during the typhoon were expected, as high wind speeds of a typhoon are known to snap and fell trees (Boucher et al. 1990; Frangi & Lugo 1991). Large canopy or emergent trees bear the brunt of the winds and their trunks snap if not sufficiently resistant. The variability in wind direction in highly heterogeneous topography (Mabry et al. 1998) presumably results in the twisting of tree trunks before breakage, as observed in Palanan. Elevated mortality of small trees during the typhoon may have been more from damage caused by falling trunks or branches than direct wind effects. In the quadrats where large diameter trees fell, smaller trees in the area beneath the felled tree could not be located. We suggest that medium-sized trees survived best because they are shielded from the heaviest winds (Imbert et al. 1996) and are also large enough to avoid being crushed by falling branches. Extensive defoliation is another effect of typhoons that has been recorded elsewhere (Brokaw & Walker 1991; Reilly 1991; Walker et al. 1991; Lin et al. 2011); this was also observed but not measured in Palanan.

A threshold value of 5% mortality per year delineates background from catastrophic mortality in tropical rain forests from the Amazon to Malaysia (Lugo & Scatena 1996). This classifies both typhoon and non-typhoon mortality rates for Palanan as non-catastrophic despite the intensity of category-four winds (>210 kph) brought by Typhoon Imbudo. In other typhoon-prone forests, much higher mortality rates have been reported in census intervals including a strong typhoon. At Kolombangara in the Solomon Islands, background rates of mortality were 1.4–2.2%$\cdot$yr^{-1} over 30 yrs (1964–1994), but mortality (median) spiked to 10.9%$\cdot$yr^{-1} soon after category-two typhoon Annie hit the island in 1967 (Burslem et al. 2000). In Puerto Rico, 7–9% tree mortality was measured in Luquillo after Hurricane Hugo (Walker 1991; Zimmerman et al. 1994), while 13% of trees died in Las Delicias, Nicaragua, during Hurricane Joan (Boucher et al. 1990). In the Cubuy forest in Puerto Rico, 7.5% annual mortality was recorded 6 months after Category 3 Hurricane Georges, whereas background mortality on non-hurricane years was 0.7% for trees ≥9.1 cm DBH (Ostertag et al. 2005). These studies included trees with a minimum DBH of only 4–5 cm, thus missing the likely higher mortality of small trees (1–5 cm DBH). Typhoon impact on tree mortality of the Palanan forest was closer to the response at the subtropical Fushan Forest in Taiwan, where mortality was 4.6%$\cdot$yr^{-1} during a period with several typhoons (Lin et al. 2011; J.M. Chiang, unpubl. data). Altogether, these comparisons indicate that Palanan had among the lowest recorded mortality rates observed following a severe tropical storm. This suggests that the typhoon-prone forest of Palanan has an assembly of tree species highly resistant to strong typhoon disturbances.

Mortality was not uniform across the 16-ha plot as topography affected the extent of typhoon damage (Reilly 1991; Boose et al. 1994). Windward habitats of the Palanan plot had higher mortality, as the windstream and windslope habitats were perpendicular to the typhoon track, whereas the leeward habitats were protected. Similar effects were recorded in Luquillo, Puerto Rico (Walker 1991) and in Jamaican montane rain forests after Hurricane Gilbert (Bellingham 1991).

Typhoon-induced tree mortality resulted in the loss of 2.64% of the total above-ground biomass within the Palanan plot as estimated with allometric equations. The biomass loss in the typhoon interval was the consequence of higher mortality in large diameter trees. After Imbudo, the Palanan forest recovered so rapidly that by 2010, biomass increased by 45.8 t$\cdot$ha^{-1} (11.5%), exceeding 1998 levels. In other forests, net loss of biomass can be far higher, as much as 50% in Puerto Rico (Scatena et al. 1993) and 76% in Nicaragua (Mascaro et al. 2005). In the Bisley Experimental Watershed of Luquillo, Puerto Rico, the level of above-ground biomass prior to Hurricane Hugo was recovered within 15 yrs with the next hurricane disturbance expected in another 45 yrs (Scalley et al. 2010). The forests near Bluefields, Nicaragua, are estimated to return to 90% of pre-hurricane AGB levels within 70–200 yrs, where a 100-yr return time for hurricanes is estimated (Mascaro et al. 2005). Again, the Palanan forest was far more resilient to storm damage than these Latin American sites. The species of trees in the Palanan forest appear to have traits that allow for a fast return-time of 6 yrs in abundance and biomass of the total forest.

Recruitment and growth

Forest recovery following typhoon disturbance can involve recruitment, release and regrowth (Everham & Brokaw 1996). Recruitment rates in the Palanan forest were three to four times higher during the typhoon interval, instead of the subsequent non-typhoon interval, as predicted. The immediate dramatic pulse of recruitment demonstrates the resilience of the forest to significant disturbance.

Recruitment into the 1–2 cm DBH class could be due to the growth of plants just smaller than 1 cm, facilitated by higher light availability from canopy defoliation within the 6–12 month post-typhoon window. Pioneer species in the genera *Clerodendrum, Ficus, Macaranga* and *Mallotus* (Fig. 5a) were major components of the recruits, causing a short-lived shift in floristic composition, as these genera subsequently declined in abundance. Scatena et al. (1996) described a similar succession following a Puerto Rico hurricane.

Two slow-growing canopy species in the family Dipterocarpaceae, *Shorea contorta* S. Vidal and *Shorea palosapis* Merr., increased in abundance by 29.7% and 14.7%, respectively, during the typhoon interval. Both species had produced many seeds and seedlings during a mast fruiting event prior to 2003 (S.L. Yap, pers. obs.). Advanced regeneration of dipterocarp seedlings can remain suppressed in the understorey for decades, awaiting more favourable light environments for growth (Scholes et al. 1997; Ashton 1998; Romell 2007). Increased light levels associated with typhoon-induced canopy defoliation appears to have released the dipterocarp seedlings in Palanan, resulting in increased recruitment to the 1 cm DBH size class. A similar pattern has been observed for post-hurricane growth in the climax species, *Manilkara bidentata* (A.DC.) A. Chev. in Luquillo forest, where post-hurricane growth rates were 17 times higher than pre-hurricane growth rates (You & Petty 1991). For *M. bidentata*, higher growth was associated with increased light on the forest floor (Fernandez & Fetcher 1991; You & Petty 1991). Although there was no massive loss of canopy trees in the Palanan forest, we speculate that typhoon-induced defoliation provided increased light availability to seedlings, facilitating both the regeneration of pioneer species and the growth release of shade-tolerant species with advance regeneration. Despite its natural tolerance for shade in the forest, *S. contorta* seedlings are known to grow well when planted in open, degraded habitats (Tomboc & Basada 1978).

Conclusions

The forest of Palanan was both highly resistant and resilient to typhoon Imbudo's disturbance. The intense, category-four typhoon caused only a small increase in mortality and small loss (2.6%) in biomass, but perhaps the more important effect was the defoliation of the canopy that led to a pulse of recruitment. The immediate recruitment of pioneer species coupled with the release of saplings of canopy species, demonstrate the resilience of this ecosystem in structure and in species composition. Increased overall light levels following the typhoon most likely led to the maintenance of stand structure via increased growth and recruitment, particularly in habitats with the higher mortality, leading to the rapid recovery of the forest to pre-typhoon conditions. The gain in biomass in 2010 from a net loss in 2004 from the effects of Typhoon Imbudo further show the resilience of this forest. In fact, the 2010 census shows a species diversity, stand structure and AGB similar to the 1998 census, just in time for Typhoon Megi that struck Palanan in October 2010. The Palanan forest is resistant and resilient to the current frequency and intensity of typhoons. Whether this forest can tolerate the increased frequency of intense typhoons, as has been projected under some global change scenarios (IPCC 2007; Stowasser et al. 2007; Knutson et al. 2010), is an important issue for the future conservation of this biodiverse ecosystem.

Acknowledgements

We thank the Department of Environment and Natural Resources (Reg. 2) for permission to conduct long-term studies in the Northern Sierra Madre Natural Park. The Palanan FDP has been supported by the University of the Philippines, Conservation International-Philippines, Isabela State University and the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute. We also acknowledge the helpful feedback from participants of the CTFS-ForestGEO workshops (supported by NSF grant DEB-1046113 to S.J. Davies), especially G. Chuyong, D. Kenfack, Y. Lin, S. Lum, S. McMahon, N. Pongpattananurak and S. Pulla, during the preliminary analysis of data. S. Russo provided insightful comments that improved the manuscript. SLY especially thanks the field workers in Palanan and the invaluable support and dedication given by the late Leonardo L. Co and Daniel A. Lagunzad, former principal investigators of the Palanan FDP, and Perry S. Ong, current plot principal investigator. SLY participated in the collection and management of census data, conducted statistical analyses and drafted the manuscript. SJD helped conceive the study, reviewed data interpretation and significantly contributed to the manuscript. RC oversaw data analysis and made important revisions to the manuscript. All authors read and approved the final manuscript. The authors declare that they have no conflict of interest.

References

Ashton, M. 1998. Seedling ecology of mixed-dipterocarp forest. In: Appanah, S. & Turnbull, J. (eds.) *A review of dipterocarps:*

taxonomy, ecology and silviculture, pp. 89–98. Center for International Forestry Research, Bogor, ID.

Bellingham, P.J. 1991. Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. *Biotropica* 23: 427–433.

Boose, E.R., Foster, D.R. & Fluet, M. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* 64: 369–400.

Boucher, D.H., Vandermeer, J.H., Yih, K. & Zamora, N. 1990. Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology* 71: 2022–2024.

Brokaw, N.V.L. & Walker, L.R. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* 23: 442–447.

Burslem, D.F.R.P., Whitmore, T.C. & Brown, G.C. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology* 88: 1063–1078.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D.F., Folster, H., Fromard, F., Higuchi, N., (...) & Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Chuyong, G.B., Kenfack, D., Harms, K.E., Thomas, D.W., Condit, R. & Comita, L.S. 2011. Habitat specificity and diversity of tree species in an African wet tropical forest. *Plant Ecology* 212: 1363–1374.

Co, L., LaFrankie, J., Lagunzad, D., Pasion, K., Consunji, H., Bartolome, N., Yap, S., Molina, J., Tongco, M., (...) & Ashton, P. 2006. *Forest Trees of Palanan, Philippines: a study in population ecology*. Megatone Printhauz Inc, Quezon City, PH.

Condit, R. 1998. *Tropical forest census plots*. Springer, Berlin, DE, and R. G. Landes Co., Georgetown, TX, US.

Condit, R., Ashton, P., Manokaran, N., LaFrankie, J., Hubbell, S. & Foster, R. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions of the Royal Society of London, Series B* 354: 1739–1748.

Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S.P. & Foster, R.B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* 20: 51–72.

Everham, E.M. III & Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* 62: 113–185.

Fernandez, D.S. & Fetcher, N. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* 23: 393–399.

Foster, D.R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* 76: 135–151.

Frangi, J.L. & Lugo, A.E. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* 23: 324–335.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.

Heaney, L.R. & Regalado, J.C. 1998. *Vanishing treasures of the Philippine rainforest*. The Field Museum, Chicago, IL, US.

Imbert, D., Labbe, P. & Rousteau, A. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. *Journal of Tropical Ecology* 12: 663–680.

IPCC. 2007. Contribution of Working Group I to the fourth assessment report of the intergovernmental panel on climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (eds.) *Climate change 2007: the physical science basis.* pp. 996. Cambridge University Press, Cambridge, UK and New York, NY, US.

Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J.P., Srivastava, A.K. & Sugi, M. 2010. Tropical cyclones and climate change. *Nature Geoscience* 3: 157–163.

Lin, T.C., Hamburg, S.P., Lin, K.C., Wang, L.J., Chang, C.T., Hsia, Y.J., Vadeboncoeur, M.A., McMullen, C.M.M. & Liu, C.P. 2011. Typhoon Disturbance and Forest Dynamics: Lessons from a Northwest Pacific Subtropical Forest. *Ecosystems* 14: 127–143.

Lugo, A.E. & Scatena, F.N. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28: 585–599.

Mabry, C.M., Hamburg, S.P., Lin, T.C., Horng, F.W., King, H.B. & Hsia, Y.J. 1998. Typhoon disturbance and stand-level damage patterns at a subtropical forest in Taiwan. *Biotropica* 30: 238–250.

Mascaro, J., Perfecto, I., Barros, O., Boucher, D.H., de la Cerda, I.G., Ruiz, J. & Vandermeer, J. 2005. Aboveground biomass accumulation in a tropical wet forest in Nicaragua following a catastrophic hurricane disturbance. *Biotropica* 37: 600–608.

Maury-Lechon, G. & Curtet, L. 1998. Biogeography and Evolutionary Systematics of Dipterocarpaceae. In: Appanah, S. & Turnbull, J. (eds.) *A review of dipterocarps: taxonomy, ecology and silviculture*, pp. 89–98. Center for International Forestry Research, Bogor, ID.

Merrill, E.D. 1926. *An enumeration of Philippine flowering plants*, Vols. I–IV. Bureau of Printing, Manila, PH.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Ostertag, R., Silver, W.L. & Lugo, A.E. 2005. Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica* 37: 16–23.

Reilly, A.E. 1991. The effects of Hurricane Hugo in three tropical forests in the U.S. Virgin Islands. *Biotropica* 23: 414–419.

Romell, E. 2007. *Artificial canopy gaps and the establishment of planted dipterocarp seedlings in* Macaranga spp.*-dominated sec-*

ondary tropical rain forests of Sabah, Borneo. Thesis, Swedish University of Agricultural Sciences, Uppsala, SE.

Scalley, T.H., Scatena, F.N., Lugo, A.E., Moya, S. & Ruiz, C.R.E. 2010. Changes in structure, composition, and nutrients during 15 years of hurricane-induced succession in a subtropical wet forest in Puerto Rico. *Biotropica* 42: 455–463.

Scatena, F.N., Silver, W., Siccama, T., Johnson, A. & Sanchez, M.J. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico before and after Hurricane Hugo, 1989. *Biotropica* 25: 15–27.

Scatena, F.N., Moya, S., Estrada, C. & Chinea, J.D. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28: 424–440.

Scholes, J.D., Press, M.C. & Zipperlen, S.W. 1997. Differences in light energy utilization and dissipation between dipterocarp rain forest tree seedlings. *Oecologia* 109: 41–48.

Stowasser, M., Wang, Y. & Hamilton, K. 2007. Tropical cyclone changes in the western North Pacific in a global warming scenario. *Journal of Climate* 20: 2378–2396.

Tomboc, C.C. & Basada, R.M. 1978. White lauan (*Shorea contorta*) in the open and under secondary growth forest canopy. *Sylvatrop* 3: 205–210.

Vandermeer, J., de la Cerda, I.G., Boucher, D., Perfecto, I. & Ruiz, J. 2000. Hurricane disturbance and tropical tree species diversity. *Science* 290: 788–791.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 379–385.

Walker, L.R., Lodge, D.J., Brokaw, N.V.L. & Waide, R.B. 1991. An introduction to hurricanes in the Caribbean. *Biotropica* 23: 313–316.

Yih, K., Boucher, D.H., Vandermeer, J.H. & Zamora, N. 1991. Recovery of the rain forest of Southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica* 23: 106–113.

You, C. & Petty, W.H. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23: 400–406.

Zimmerman, J.S., Everham, E.M. III, Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* 82: 911–922.