

# Less diverse forest is more resistant to hurricane disturbance: evidence from montane rain forests in Jamaica

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## Summary

**1** Are more diverse ecosystems more or less resistant to disturbance? Does diversity increase in a forest after being hit by a hurricane? We answer these questions using a 30-year study of four Jamaican forests, which differ in soil fertility and diversity, and which were hit by Hurricane Gilbert in 1988; the decades were: pre-Gilbert (1974–84), Gilbert (1984–94), and post-Gilbert (1994–2004).

**2** Diversity (Shannon index) was always higher in the three forests (Col H' 3.00, Mull H' 2.91 and Slope H' 2.99) on more fertile soils (C : N ratios 10–13, N : P 16–24), and significantly lower in the Mor forest (H' 2.26) with the least fertile soil (C : N ratio 24, N : P ratio 44). Diversity increased during the Gilbert decade in two of the more diverse forests (Mull and Slope), it did not increase in the least diverse, Mor forest. The overall increase in diversity during the Gilbert decade was due to the recruitment of eight, mostly light-demanding, species and the increased abundance of uncommon species.

**3** We used turnover rates (the average of mortality and recruitment of stems) as a measure of resistance. We equate low turnover with high resistance to hurricane damage. Turnover increased during the Gilbert decade in all forests, but increased more in the three more diverse forests (Mull 1.5% year<sup>-1</sup> 1974–84 to 3.1% year<sup>-1</sup> 1984–94; Slope 1.3–2.6; Col 1.5–3.2); than in the least diverse Mor forest (1.2–1.9).

**4** Stem diameter growth rates pre-Gilbert were very low in all forests and were lowest in the Mor forest (Mor 0.3 mm year<sup>-1</sup>, Mull 0.4, Slope 0.5, Col 0.6). They increased during the Gilbert decade and remained, in the post-Gilbert decade, double those of the pre-Gilbert decade (Mor 0.6 mm year<sup>-1</sup>, Mull 0.6, Slope 0.8, Col 1.1). Smaller stems increased growth more than larger stems. The stems recruited during the Gilbert and post-Gilbert decades grew faster than those present in 1974.

**5** Thus, in montane forest in Jamaica the least diverse forest was most resistant to hurricane damage, and although there was a strong similarity in species rank abundances over 30 years including a hurricane, the hurricane increased diversity.

*Key-words:* diversity, hurricanes, mortality, recruitment, resistance

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## Introduction

Natural disturbances affect all ecosystems, killing all or some resident organisms and disrupting ecosystem processes. With global loss of biodiversity a pressing issue, determination of relationships between ecosystem diversity and response to disturbance is of particular interest: this has been the subject of studies over many years (MacArthur 1955; Hooper *et al.* 2005). However

predictions of relationships between diversity and response to disturbance remain elusive. While one recent review concluded that 'communities with greater diversity tend to be stable', with stable meaning 'less oscillatory and less susceptible to invasion by exotic species' (Tilman *et al.* 2001), others have concluded the opposite (Goodman 1975).

Responses to disturbance may be anywhere in the space defined by the following two axes: (i) resistance ('staying essentially unchanged', Grimm & Wissel 1997); and (ii) resilience ('returning to a reference state', Grimm

& Wissel 1997). Disturbances may be of many kinds, for example wind, drought, flooding, fire, freezing and herbivores, and attempts to generalize about how ecosystems respond to disturbances, across different disturbances and different ecosystems, are likely to have many exceptions. If for no other reason, because different disturbances cause different communities, for example in an area of hundreds of hectares, with access to the same species pool, an ecosystem disturbed by wind is likely to be very different to an ecosystem disturbed by flooding. In addition, some recent experimental studies of the relationship between diversity and ecosystem properties have studied the first disturbance to affect the ecosystem (Tilman 1996). It is likely that natural ecosystems have recurrent disturbances and that susceptible species will have become locally extinct, or have small population sizes, by the time a study of a particular natural disturbance event is made. Thus, patterns in nature will probably be very different from patterns discovered in relatively short-term experiments. Finally, it has been shown that it is not diversity itself that defines ecosystem responses to disturbance but the properties of the species in the ecosystem (Sankaran & McNaughton 1999).

There are very few studies of how natural systems that differ in diversity are affected by natural disturbances, and even fewer of forests despite the likelihood that major disturbances determine the species composition of large areas of forest (Oliver 1980). Tropical rain forests are among the earth's most diverse ecosystems, and many are subject to major disturbances such as hurricanes, which have major effects on their growth and composition (Everham & Brokaw 1996). Research into the effects of hurricanes shows that while some of the initial effects are destructive, some of the longer term, decadal, effects may be positive, for example increased growth of surviving trees has been reported following hurricanes (Merrens & Peart 1992; Bellingham *et al.* 1995; Scatena *et al.* 1996; Batista & Platt 2003).

The effects of disturbance on diversity in tropical rain forests have been less well studied. In Kolombangara, plots with higher diversity suffered more canopy damage and had higher recruitment and turnover of the 12 commonest species (only 12 species were recorded after 1964) following two cyclones in the 6 years after the start of the study in 1964 (Burslem & Whitmore 1999). In Nicaragua a comparison of diversity between five forests, four in one area hit by a hurricane and one in an area not hit by the hurricane, showed higher diversity in the hurricane damaged forests (Vandermeer *et al.* 2000). A 54-year study of a plot in Puerto Rico concluded that the high diversity when the plot was established was due to a hurricane 15 years previously, though a hurricane hit in 1998 caused no increase in diversity in that plot by 2000 (Weaver 2002). None of these studies have unambiguously shown increased diversity caused by a hurricane (or cyclone) for different reasons: Burslem & Whitmore (1999) had no complete species records after their cyclones; Vandermeer *et al.* (2000) had no pre-hurricane records;

and though Weaver (2002) had pre- and post-hurricane records he found no increase in diversity.

Our study has both pre- and post-hurricane records collected over a 30-year period from permanent plots in four Jamaican montane rain forests. We address the question of whether there is a relationship between tree species diversity (on the one hand) and resistance and resilience (on the other), using a natural gradient of diversity/fertility and a natural disturbance, a hurricane. In addition to the between-forest comparison of diversity and resistance and resilience we report on the overall effect of the hurricane on diversity and growth, by using the combined data set from the four forests. Thus, our null hypotheses are: (i) that there was no relationship between diversity on the one hand and resistance and resilience on the other; (ii) that diversity was unchanged by hurricane damage; and (iii) that growth was unaffected by hurricane damage.

## Methods

### FORESTS, TREES AND SOILS

We studied four Jamaican upper montane rain forests within 300 m of each other (18°05' N, 76°39' W; 1580–1600 m): Col forest (Gap forest of Tanner 1977, 0.09 ha sampled); Wet Slope forest (0.1 ha); Mull Ridge forest (0.1 ha) and Mor Ridge forest (0.06 ha); hereafter abbreviated to Col, Slope, Mull and Mor (the 'forests' in the current paper are the 'sites' of Tanner 1977). The forests were selected in 1974 (for a study of nutrient cycling) as representative of forests in the western Blue Mountains, the first 10 × 10 m plot in each forest was subjectively positioned in 'representative' forest, the other plots in each forest were contiguous. All stems ≥ 3 cm d.b.h. (at 1.3 m) in permanent 10 × 10 m plots were tagged, painted with a ring at 1.3 m, identified, and measured in 1974, 1984, 1989, 1991, 1994 and 2004. Multi-stemmed trees were recorded. In total we had 2745 stems, 2171 individuals and 68 species; nomenclature follows Adams (1972), except where other authorities are listed. Soil (0–10 cm depth) total C, N (CHN analyser), P (acid digest) and Bray 1-extractable P were determined by Brookside Laboratory Association Inc. (Knoxville, Ohio, USA) from cores collected and air-dried in July and August 2004, from three randomly chosen plots per forest.

### HURRICANE GILBERT

Hurricane eyes pass over, or within 15 km of, the Blue Mountains of Jamaica on average every 25 years. During our study period (1974–2004) Hurricane Gilbert struck in 1988; it was the most powerful hurricane recorded in the Caribbean during the 20th century (Dodge *et al.* 1999). The hurricane killed about 2% of stems in these forests 'immediately' (Bellingham *et al.* 1992) and 13% over a 16-year period. It uprooted 5% of stems, broke crowns from 4% of stems and completely defoliated 19%

of stems, thus increasing light availability at the forest floor for up to 33 months after the hurricane (Bellingham *et al.* 1995, 1996). We report results over three decades with respect to Hurricane Gilbert: pre-Gilbert decade (1974–84), Gilbert decade (1984–94), and post-Gilbert decade (1994–2004).

#### DATA ANALYSES

For the tree stems (not the individuals) we report Fisher's alpha ( $S = \alpha \ln(1 + N/\alpha)$  where  $S$  = number of species in the sample,  $N$  = number of stems in the sample,  $\alpha$  = Fisher's alpha) and the Shannon index,  $H'$  (the negative sum over all species of  $(q_i/Q)\ln(q_i/Q)$ , where  $q_i$  = abundance of  $i$ th species,  $Q$  = total number of stems in the sample). We statistically compared  $H'$  between (unreplicated) forests following the worked example in Magurran (1988); in our data cumulative  $H'$  changed less than 5% after using two plots in each forest. We carried out rarefaction procedures using the ECOSIM program (Gotelli & Entsminger 2006), in which we used the number of stems (1716) per species in 1984 (Appendix S1 in Supplementary Material) to estimate the number of species for 1716 stems from the data sets for 1994 and 2004. For each decade we calculated mortality, recruitment and turnover. Mortality as percentage is:  $100(m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t})$ , where  $N_0$  = number at the beginning of a period,  $N_1$  = number of survivors at the end of a period, and  $t$  = time in years. Recruitment as percentage is:  $100(r = 1 - (1 - N_r/N_t)^{1/t})$ , where  $N_r$  = number of recruits during a period and  $N_t$  is the number at the end of the period. Turnover is the average of mortality and recruitment. All comparisons of mortality and recruitment were across equal decade intervals so problems in assessing rates across different census intervals were avoided (Kohyama & Takada 1998). Mortality and recruitment of stems were compared between forests using contingency tables. We used regression analysis to compare the number of tree stems per species in 1984 with those in 2004 and compared the fitted line with a null hypothesis relationship of 1 : 1. We compared the gains and losses of species overall (all forests combined) using a binomial test, with the null hypothesis that the number of species recruited should equal the number lost. We calculated Euclidian distances to show departure from initial biomass composition as in Lepš *et al.* (1982), biomass calculated using equations in Tanner (1980). The mean trunk diameter growth rates were compared between forests within a decade by Mann–Whitney  $U$ -tests and between decades by paired  $t$ -tests. To discover whether differences in trunk growth rates before and after the hurricane were related to trunk size, we calculated, for the 977 trunks alive in 1974 and 1991, the mean absolute growth in trunk diameter from 1974 to 1984 and divided it by 10, and the mean absolute growth in trunk diameter from 1989 to 1991 and divided it by 2. We plotted the difference between these two absolute rates against trunk diameter in 1989 and fitted a linear regression; we compared the intercept and slope of the fitted line against a null hypothesis of zero for both.

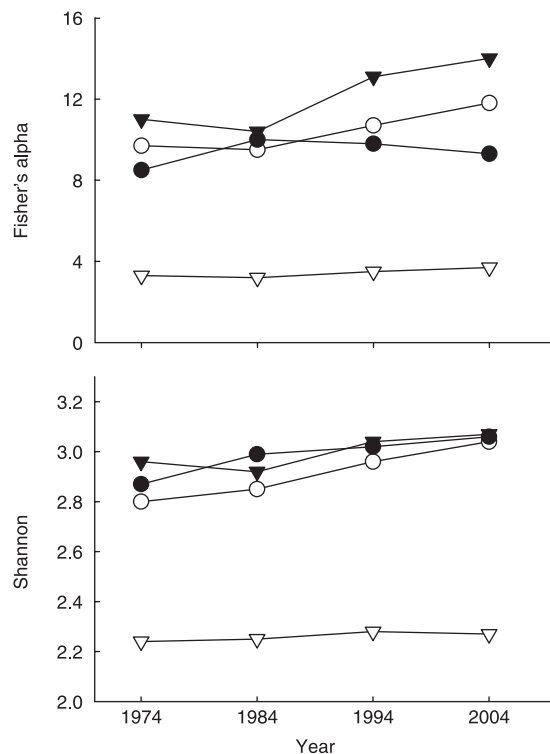


Fig. 1 Fisher's alpha and Shannon indices of diversity for the four forests: ● = Col; ▼ = Slope; ○ = Mull; ▽ = Mor.

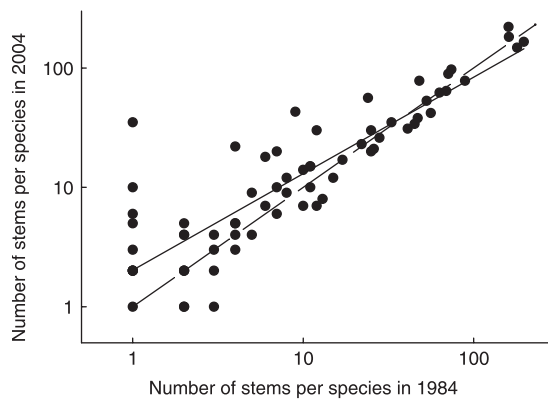
## Results

### DIVERSITY, RECRUITMENT, MORTALITY AND GROWTH IN THE FOUR DIFFERENT FOREST TYPES

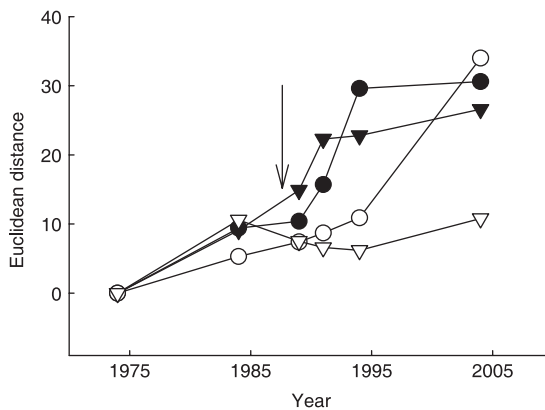
Diversity was always highest in the three forests on more fertile soils (Fig. 1) with lower C : N and C : P ratios (Table 1); diversity was significantly lower in the Mor with very infertile soil (comparisons of  $H'$  for 1984: Mor vs. Mull,  $t_{1065} = 9.4$ ,  $P < 0.001$ ; Mor vs. Col,  $t_{617} = 10.3$ ,  $P < 0.001$ ; Mor vs. Slope,  $t_{730} = 9.7$ ,  $P < 0.001$ ; all other comparisons not significant). Diversity increased after the hurricane in two of the three forests on more fertile soils (Mull and Slope); in contrast, the least diverse Mor forest showed no change in diversity throughout the study (Fig. 1). Summed over the four forests there was an increase in diversity in response to the hurricane (Fig. 2, Appendix S1) due to the net recruitment of species not previously recorded in the plots (but present, though rare, in the surrounding forest). The increase in diversity was a result of the increase in the number of stems because rarefaction analyses, when the number of stems was kept constant, gave no statistically significant increase in species post-Gilbert. Between 1984 and 1994, eight species were recruited and none were lost (exact binomial test,  $P = 0.01$ ); all these species were occasional or rare in 1994 (occasional and rare = lower 40% of species in terms of rank abundance), except for the invasive alien tree *Pittosporum undulatum*, which by 2004 was, in terms of individuals, the 17th most abundant species of 65 (Appendix S1). The changes in populations of trees resulted in a drift

**Table 1** Soil (0–10 cm) nutrient concentrations, mean values from one core from each of three randomly chosen plots per forest

Forest	N (%) total	C (%) total	P (%) total	C : N total	C : P total	N : P total	P (p.p.m.) 'Bray 1'	Bulk density (g cm <sup>-3</sup> )
Col	1.1 ± 0.12	11.0 ± 1.4	0.07 ± 0.01	10 ± 0.3	161 ± 17.8	15.7 ± 1.3	14.0 ± 0.6	0.6 ± 0.03
Slope	0.68 ± 0.08	9.1 ± 1.5	0.04 ± 0.01	13 ± 0.8	282 ± 129	20.4 ± 8.7	11.0 ± 1.1	0.7 ± 0.2
Mull	0.88 ± 0.10	11.6 ± 1.5	0.04 ± 0.01	13 ± 0.4	317 ± 13.2	23.7 ± 5.5	8.3 ± 0.3	0.5 ± 0.1
Mor	2.0 ± 0.03	49.0 ± 1.2	0.05 ± 0.00	24 ± 0.9	1056 ± 55	43.8 ± 3.5	6.7 ± 0.3	0.08 ± 0.02



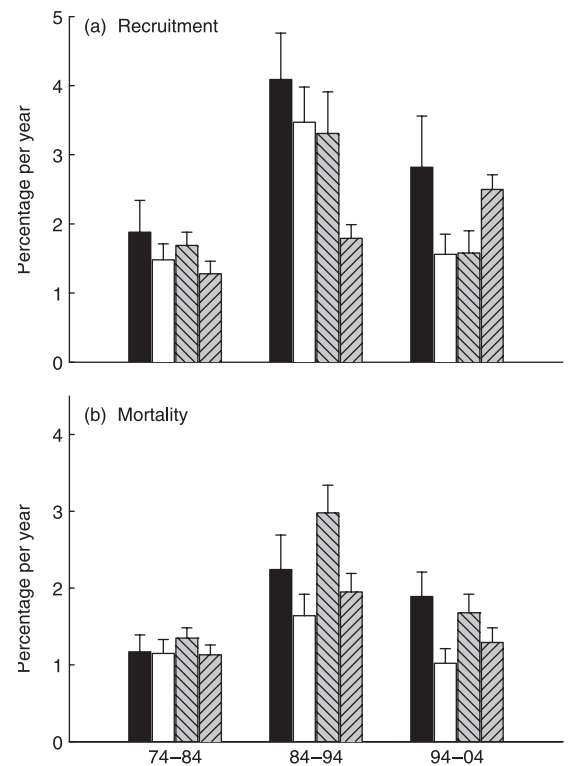
**Fig. 2** The number of stems per species (+1 to allow a log log plot) in 1984 and 2004; solid line is best-fit line ( $y = 0.80$  (SE 0.055),  $x + 0.32$  (SE 0.064)). The slope of the line is significantly less than 1.00 ( $P < 0.05$ ), and the intercept is significantly greater than 1.00 ( $P < 0.01$ ), the expectation if numbers of stems per species were the same in 1984 and 2004 (dashed line); thus species were recruited, rare and uncommon species increased and common species were unchanged.



**Fig. 3** Euclidean distance to show departure from initial composition using data for biomass per species in each forest, calculated as in Lepš *et al.* (1982): ● = Col; ▼ = Slope; ○ = Mull; ▽ = Mor; arrow denotes impact of Hurricane Gilbert in 1988.

away from the initial biomass composition, but less so in the least diverse Mor forest (Fig. 3).

Mortality rates did not differ between the forests in the pre-Gilbert decade (Fig. 4, Appendix S2); they increased in all four forests during the Gilbert decade but increased less in the Mor and Slope than in the Mull and Col (Fig. 4). Recruitment rates in the pre-Gilbert decade were lower in the Mor than the Mull and Col forests



**Fig. 4** (a) Percentage recruitment of stems and (b) percentage mortality of stems, in each of four forests in three decades; mean per forest and standard error of the mean to show the variation between plots within a forest. The variation between forests (compared by contingency tables) was not significant ( $P > 0.05$ ) for mortality or recruitment from 1974 to 84, but was significant for both mortality and recruitment in both 1984–94 and 1994–2004. ■ = Col; □ = Slope; ▨ = Mull; ▩ = Mor.

(Fig. 4, Appendix S2) and, like mortality, increased during the Gilbert decade but much less in the Mor (Fig. 4, Appendix S2). Thus, the three forests on more fertile soils were the most dynamic; that is, they had higher turnover rates (mean of mortality and recruitment) than the Mor, in the Gilbert decade (Fig. 4, Appendix S2).

Across the four forests, 38% of the stems present in 1974 had died by 2004, and 47% of the stems present in 2004 were recruits since 1974; 32% of the basal area present in 1974 was dead by 2004, but only 3% of the basal area in 2004 was recruited since 1974.

Stem diameter growth was very slow in all forests, but especially so in Mor (Mor 0.3 mm year<sup>-1</sup>, Mull 0.4, Slope 0.5, Col 0.6 from 1974 to 1984, Fig. 5); diameter growth increased during the Gilbert decade and remained

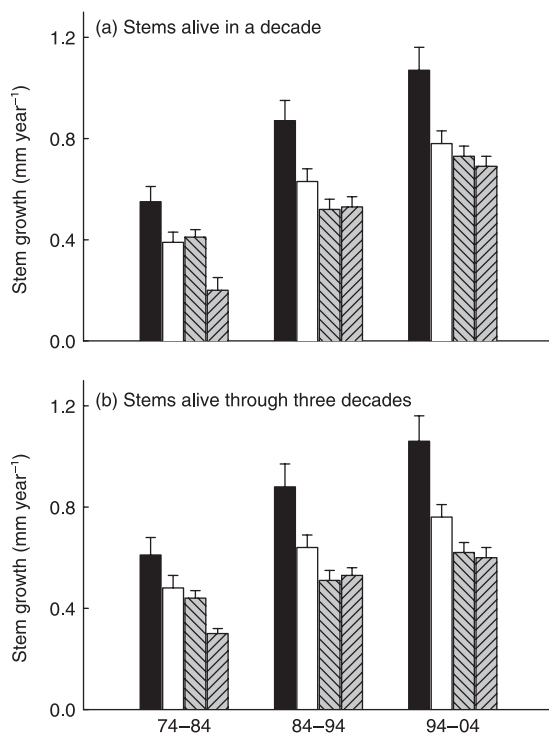


Fig. 5 The absolute diameter growth rate of stems (mean  $\pm$  SE), in each forest and in each decade; (a) stems alive in a particular decade; (b) stems alive throughout, i.e. in 1974, 1984, 1994 and 2004. ■ = Col; □ = Slope; ▨ = Mull; ▩ = Mor.

higher in the post-Gilbert decade 1994–2004 (Mor  $0.6 \text{ mm year}^{-1}$ , Mull  $0.6$ , Slope  $0.8$ , Col  $1.1$ , Fig. 5). The increased growth was very marked in Mor and Col; pre-Gilbert growth was significantly lower in Mor compared with the other three forests, but in the last decade stem growth in the Mor was not significantly lower than in the others (Appendix S3). Furthermore, in those stems present from 1974 to 1991, growth in the Gilbert and post-Gilbert decades increased more in smaller than larger stems (Fig. 6, Appendix S4). The stems recruited during the Gilbert and post-Gilbert decades grew faster both absolutely (compare Fig. 5a with Fig. 5b) and relative to trunk size than those present pre-Gilbert.

## Discussion

### DIVERSITY AND DYNAMICS ACROSS THE FOUR FORESTS

Mor forest, the least diverse throughout the study, is on the crest of the main ridge of the Blue Mountains and was as exposed to the hurricane as any of the four forests. Although we studied in detail only one Mor forest, which limits the statistical tests we can carry out, it is very similar in species composition and physiognomy to other Mor forests within 5 km. Despite the fact that 10.1% of surviving stems in the Mor forest were severely damaged (defined as trees tipped up to  $> 40^\circ$  from their pre-hurricane position and/or crown death) by the hurricane (vs. 9.5% in the Mull forest, 7.0% in the Col forest, and

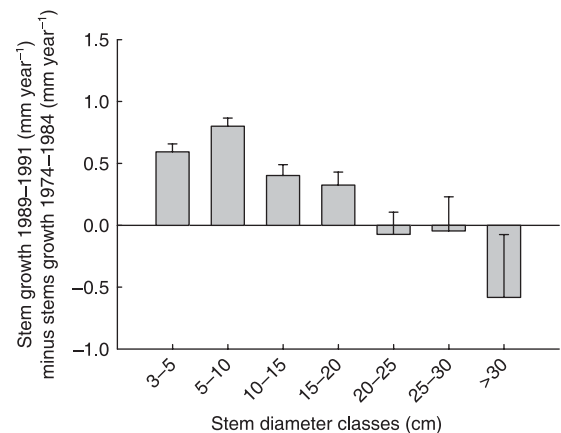


Fig. 6 Difference between mean annual absolute stem diameter growth 1989–91 and mean annual absolute growth 1974–84 ( $\text{mm year}^{-1}$ ), by stem size classes, for those stems alive in both 1974 and 1991 (mean and SE).

5.8% in the Slope forest), the Mor forest had lower turnover than the other three forests. The low turnover was probably a result of at least five factors. First, the species in the Mor are less susceptible to being killed by the hurricane. Evidence for this comes from the Mull, where for the 277 individuals of species that also grow in the Mor mortality was 16% (1984–94); in contrast, for the 245 individuals of species which grew in the Mull but not the Mor, mortality was 35% ( $\chi_1^2 = 24.7$ ,  $P < 0.0001$ ) (though there was no relationship between mortality per species and wood density, just as there was no correlation between wood density and damage due to the hurricane, Bellingham *et al.* 1995). Secondly, multiple-stemmed trees, which were more prevalent in the Mor forest than the others (in 1974 38% of individuals in Mor forest had multiple stems vs. 9–17% in the other three forests;  $\chi_3^2 = 93$ ,  $P < 0.0001$ ), have a lower chance of dying than single stemmed trees (of 1126 individuals with single stems 21% died between 1984 and 1994; in contrast, of 227 trees with multiple stems only 8% died;  $\chi_1^2 = 14.4$   $P < 0.0001$ ). Thirdly, there was a high incidence of sprouting by most of the dominant species of the Mor (Bellingham *et al.* 1994), which reduced individual mortality. Fourthly, the Mor forest has shorter trees; this probably resulted in less wind-caused mortality. Fifthly, low mortality in the Mor forest was probably partly a result of the weak, *c.* 50-cm deep, mor humus that allowed the trees to flex in the wind, thus reducing their canopy damage (although there was substantial crown damage to one common tree in this forest, *Cyrilla racemiflora*, Bellingham *et al.* 1995). The other half of ‘turnover’ is recruitment, this was also lower in the Mor, due to the very infertile, acidic (pH *c.* 3.0) mor humus, which we hypothesize limits the number of species that can grow in the forest (Grubb & Tanner 1976). Evidence supporting this hypothesis comes from an experimental clearing of  $10 \times 10 \text{ m}$  in the Mor forest; 10 years after its creation the zone from which mor humus had been removed, exposing the subsoil, had seedlings of 14 tree

species, and 13 seedlings  $\text{m}^{-2}$ ; in contrast, undisturbed mor humus had only six species and seven seedlings  $\text{m}^{-2}$  (Sugden *et al.* 1985). We conclude that characteristics of the species dominating the Mor forest are the cause of the high resistance and low resilience to hurricane damage, not low diversity *per se*.

Mor forests are atypical in composition, structure and response to Hurricane Gilbert (our Mor was resistant not resilient) among Jamaican montane rain forests. Why are resistant forests like the Mor forest not more widespread? We think it is because in the steep Blue Mountains there are very limited areas in which deep acidic litter can accumulate and the process of feedback begin and be maintained; even on ridge crests such forests are confined to knolls. However, in places where topography does not limit litter accumulation and where hurricane disturbance is frequent, the 'resistant' syndrome we found in Mor forest also appears to be uncommon (e.g. lowland Nicaragua, Vandermeer *et al.* 2000). Nutrient-limited forests in Hawaii were found to be more resistant to hurricane damage and less nutrient-limited forests more resilient (Herbert *et al.* 1999). We propose that at a landscape scale, nutrient supplies have to be limiting (as shown by low leaf nutrient concentrations in montane rain forests), which promotes the colonization by trees typical of low nutrient systems (e.g. the Ericales), and within such areas some sites will be especially nutrient poor and by feedback mechanisms generate mor soils and forests with their distinct species composition, which are resistant to hurricane damage.

#### INCREASE IN DIVERSITY AFTER THE HURRICANE

Forests on more fertile soils than Mor forests were characteristically resilient to hurricane damage. In these forests, diversity increased after hurricane disturbance as a result of an increase in abundance of uncommon species and recruitment of species not previously recorded in the plots. These two phenomena are the same; it is a matter of the scale at which the effect is measured. If the plots had included all the forest in the area, the effect would have been only an increase in abundance of the rare and uncommon species. The promotion of the uncommon species was a result of two patterns. First, the canopy trees present in 1974 were mostly of more light-demanding species that largely lacked seedlings in the understorey. Of the 10 most common trees, two had no seedlings and five had few seedlings before Hurricane Gilbert (Healey 1990). Secondly, the damage to the canopy trees allowed more light to reach the lower layers of the forest, promoting germination of seeds of light-demanding species and the growth of the seedlings and saplings of the advance regeneration into the recorded minimum size class (3 cm d.b.h.). Most of the species that increased in abundance during the Gilbert decade were light-demanding species (for example *Hedyosmum arborescens* and *Alchornea latifolia*), though one very shade-tolerant tree also increased (*Eugenia virgultosa*).

Furthermore, we judge that most of the nine species that were recruited after the hurricane were light demanding, although we have little detailed information about their ecology (almost by definition because they were mostly rare): two are definitely light demanding (*Brunellia comocladifolia* and *Miconia dodecandra*), four are likely to be light demanding (*Cestrum hirtum*, *Critonia parviflora*, *Rhamnus sphaerospermus* and *Sapium harrisii*), and two we cannot judge. However, one common recruit, *Pittosporum undulatum*, which is an invasive alien, has very shade-tolerant seedlings (Bellingham *et al.* 2005). Thus, the hurricane mostly promoted light-demanding species, but at least two shade-tolerant species also increased in abundance.

We think it likely that many hurricane-affected forests will show an overall increase in diversity after hurricanes. Indeed, any forest where the canopy trees have a lower diversity than the advance regeneration, a pattern true for most tropical forests on a scale of hundreds of square metres, is likely to show an increase in diversity after major wind storms, which severely damage the canopy and increase light and thus growth of the more species-rich advance regeneration. Such a response follows general predictive models of short-term responses to disturbance (Connell 1978; Huston 1979) and agrees with predictions from a modelling study of higher diversity in hurricane-damaged forest in Puerto Rico (Doyle 1981).

The theoretical predictions that hurricane disturbance will increase diversity find some support in the literature. Hurricane-affected forests had higher diversity compared with a less affected forest in lowland Nicaragua (Vandermeer *et al.* 2000). In Kolombangara, plots that were more damaged by cyclones had increased recruitment and turnover of the 12 commonest species, but effects on overall diversity were not recorded (Burslem & Whitmore 1999). However, a 54-year study of diversity (1946–2000) before and after hurricane damage in a permanent plot in Puerto Rico did not show an increase in diversity following two hurricanes, in 1989 and in 1998 (Weaver 2002). The lack of increase might be due to the short interval, in which case later enumerations may reveal an increase, or it could be due to the dominance of two very light-demanding species (*Cecropia schreberiana* and *Psychotria berteriana*) among the trees recruited after the hurricane. If so, there may be areas in that forest where increased light due to canopy damage was enough to strongly promote the growth of pre-existing seedlings but not so high that the seedling populations were dominated by one or two strongly light-demanding species. Short-term increases in diversity have also been found after other kinds of disturbance in tropical rain forests, such as logging, again due in part to recruitment of light-demanding species (Molino & Sabatier 2001). Recently it has been shown that in tropical rain forests without large disturbances, populations of rare species, in small quadrats, survive and grow better than those of common species (Wills *et al.* 2006); however, note that this study differs from the previous studies because recruits were not included in the analysis by Wills *et al.*

Thus it seems that rare species fare better than common species in a whole range of disturbance regimes.

#### STABILITY OF RELATIVE ABUNDANCES OF SPECIES IN RAIN FORESTS DAMAGED BY HURRICANES

Despite the significant increase in rare and uncommon species in Jamaica, and despite the fact that approximately half of the stems present in 2004 were recruits since 1974 (and 32% of the basal area present in 1974 was dead by 2004), there was a strong rank correlation in species abundance between 1974 and 2004 ( $r_{s,69} = 0.86$ ,  $P < 0.001$ ). The strong correlation in species composition in Jamaica, across 30 years including a major hurricane, is similar to the pattern across 54 years in Puerto Rico (with hurricanes 45 and 52 years into the study, Weaver 2002), and similar to the pattern for the 12 most common species across 30 years in Kolombangara (with four cyclones, only two of which damaged the forests, 3–6 years after the study started, Burslem *et al.* 2000). Thus, even in hurricane-damaged forests the major pattern is for species composition to change little over decades.

#### RESISTANCE AND RESILIENCE IN RELATION TO DISTURBANCE—GENERAL PATTERNS

Our results from Jamaica show more resistance to hurricane damage in our least diverse forest. A similar pattern was found across two forests in Puerto Rico, where higher-altitude lower-diversity forest was more resistant than higher-diversity lower-altitude forest (Walker *et al.* 1996). In Jamaica, resilience was also lower in the least diverse forest when judged by recruitment of stems during the Gilbert decade, though perhaps this is best seen as a delayed resilience because recruitment increased in the Mor in the post-Gilbert decade. Growth increase in the surviving stems post-Gilbert, another form of resilience, was also higher in Mor forest. Thus, our results do not support the conclusion of Tilman *et al.* (2001) that 'communities with greater diversity tend to be stable'. Hoping for a generalization across very different ecosystem types (forest to grasslands, e.g. this study vs. Kahmen *et al.* 2005), and across different disturbances (wind to drought), and across natural systems previously exposed to disturbances as compared with experiments where the first disturbance is studied, is probably too much, though it will probably be possible to generalize for subsets of these categories. Our results from forest in one area of the world show that low diversity was associated with high resistance to disturbance by wind.

#### Conclusion

In summary, although many initial effects of hurricanes on forests are destructive, because trees are destroyed, crown areas reduced and emergent crowns destroyed (Brokaw *et al.* 2004), this very destruction increases light

for smaller trees, thus increasing growth, and in this study, diversity. Comparisons between forest differing in diversity show that if there is an emerging pattern, it is that least diverse forests are more resistant to severe wind damage.

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### Supplementary material

The following Supplementary material is available online from [www.Blackwell-Synergy.com](http://www.Blackwell-Synergy.com)

**Appendix S1** The number of stems of each species in 1974, 1984, 1994 and 2004.

**Appendix S2** The statistical tests comparing: mortality (a), recruitment (b) and turnover (c) between forests in the three decades.

**Appendix S3** Mean diameter growth rates per decade for stems in the four forests alive in 1974 and 2004.

**Appendix S4** The difference between the absolute annual stem diameter growth 1989–91 and that from 1974 to 84, plotted against the stem diameter size in 1989.



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