RESEARCH ARTICLE

Patch dynamics and community metastability of a subtropical forest: compound effects of natural disturbance and human land use

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Abstract Where large disturbances do not cause landscape-wide mortality and successional change, forested ecosystems should exhibit landscape meta-stability (landscape equilibrium) at a scale equal to the dominant patch size of disturbance and recovery within the landscape. We investigated this in a 16-ha contiguous plot of subtropical wet forest in Puerto Rico, the Luquillo Forest Dynamics Plot (LFDP), which experienced two major hurricanes during the 15-year study and has a land use history (logging and agriculture 40 or more years hence) that differs in intensity between two areas of the plot. Using he LFDP as our "landscape," we studied the spatial pattern of community change through time (3–5 year intervals) by calculating community dissimilarity between tree censuses for two size classes of trees (1 to <10 cm DBH and ≥10 cm DBH) in quadrats ranging in size from 0.010–1 ha and for the entire landscape, i.e., plot or land use type. The point at which the decline in community dissimilarity with quadrat size showed maximum curvature identified the dominant patch size (i.e., point of metastability). For canopy trees ≥10 cm dbh, there was no evidence that the community experienced landscape-wide successional changes in either land use type, and we found a consistent patch size of community change around 0.1 ha (range 0.091–0.107). For the understory tree and shrub community (1 to <10 cm dbh) there was some evidence of landscape-wide community changes over time in response to hurricane damage, apparently driven by interactions with the dominant canopy species, whose composition varied with land use intensity, and their species-specific susceptibility to hurricane damage.

Keywords Hurricane · Landscape dynamics · Luquillo Experimental Forest · Puerto Rico · Succession · Tropical forest

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Introduction

A major goal of ecology is to link the patterns observed in populations, communities, and ecosystems to the processes that generate them (Watt 1947). Hierarchical patch dynamics (Pickett et al. 1992; Wu and Loucks 1995) is a theoretical framework that allows ecologists to understand community and ecosystem dynamics in a manner that separates the spatial and temporal dynamics of disturbance and community recovery (Turner et al. 1993). The patch dynamics paradigm proposes that ecosystem dynamics can be understood as a composite of different sized patches, defined by abiotic or biotic attributes, that change over space and time (Wu and Loucks 1995). The aim is to identify the temporal and spatial scales at which a system is stable even if the component parts are changing as a result of disturbance and recovery (Peterson et al. 1998; Fraterrigo and Rusak 2008). This concept is known in landscape ecology as metastability or landscape equilibrium (Turner et al. 1993).

Hurricanes are considered large-scale, infrequent disturbances (Romme et al. 1998; Turner et al. 1998; Lugo 2008) that, by virtue of their size, should generate qualitatively different landscape dynamics than disturbances such as tree fall gaps that are smaller and distributed across a landscape (Levin and Paine 1974; Bormann and Likens 1979). Observations of forest damage after a hurricane, however, indicate that the damage is patchy at a scale of 10–100 s of meters (Brokaw and Grear 1991; Fernández and Fetcher 1991; Boose et al. 1994; Turner et al. 1997; Platt et al. 2000). The resultant "patchiness" of hurricane disturbance to forest canopies, despite the dramatic large scale damage to canopies and stems that initially impresses the observer, may have several exogenous and endogenous causes, including vortical wind behaviors ("microbursts"), topography, spatial distributions of susceptible trees, or an autogenically determined disturbance size (Watt 1947; Platt et al. 2000; Bellingham 1991; Solé and Manrubia 1995; Ogle et al. 1996; Kellner and Asner 2009).

In tropical forests, hurricanes do not always cause high tree mortality (Bellingham et al. 1992; Everham and Brokaw 1996; but see Basnet et al. 1991 for a counterexample) and surviving trees rapidly reestablish the forest canopy (Yih et al. 1991; Bellingham et al. 1994; Zimmerman et al. 1994; Scatena et al.

1996). These observations suggest that hurricanes are not always "severe" in the sense that the term is often used (Turner et al. 1993; 1998; Romme et al. 1998; Freelich and Reich 1999) that is, causing widespread and uniform tree mortality. Winds associated with a major hurricane (Category 3 or higher hurricane on the Saffir-Simpson scale; NWS 2009), while not necessarily causing widespread tree mortality, do cause significant damage to vegetation and set in motion rapid changes in forest composition, particularly in the understory (Everham and Brokaw 1996; Scatena et al. 1996; Comita et al. 2009). The patchiness of hurricane damage and rapid recovery suggests that a forest community recovering from hurricane disturbance should exhibit a patch structure more like Bormann and Likens's (1979) mosaic-steady state concept than the broadscale yet unpredictable landscape dynamics proposed to occur after a "large, infrequent disturbance" (Turner et al. 1993; Romme et al. 1998; Turner et al. 1998; Freelich and Reich 1999).

Of particular interest to ecologists is how disturbance history alters the spatial scale of community stability over time (Wu and Loucks 1995; Foster et al. 2003). For example, hurricane disturbance may alter the spatial scale of metastability by producing a more uniform stand of trees with smaller, more compact and, therefore, hurricane-resistant canopy compared to forests without a history of hurricane disturbance (Peart et al. 1992; Brokaw et al. 2004). Human disturbance, such as logging or agriculture, may also alter the scale of metastability by producing stands dominated by secondary forest species that are highly vulnerable to wind damage because of their low wood densities (Zimmerman et al. 1994; Thompson et al. 2002; Curran et al. 2008). When vulnerable secondary species are aggregated in space, patches disturbed by hurricanes will also be spatially aggregated to create larger areas of damaged forest. The resultant landscape-level increase in propagule availability for these species, further opportunities for the recruitment of secondary species to the canopy, and the spatial aggregation of vulnerable species would over time reach a point where landscape-level changes in communities would predominate over patch-level changes (Turner et al. 1993; Freelich and Reich 1999). Thus, hurricane and human disturbance may interact to alter fundamentally the temporal and spatial scaling of community dissimilarity.

This study considers the spatial scaling of temporal community change in the 16-ha Luquillo Forest Dynamics Plot (LFDP; Thompson et al. 2002, 2004), located in subtropical wet forest in eastern Puerto Rico. The plot was established in 1990 in a forest that has been subjected to disturbance by two major hurricanes in the last two decades (Hugo in 1989 and Georges in 1998; Zimmerman et al. 1994; Uriarte et al. 2004, 2005, 2009) and parts of which were subject to logging and agriculture in the first half of the 20th century. Historical land-use has produced areas of the LFDP where secondary species dominate (García-Montiel 2002; Thompson et al. 2002). Thus, the LFDP is an ideal setting to study the interactive effects of hurricane and human disturbance on forest community dynamics (Uriarte et al. 2009) in the landscape that the plot represents.

Using spatially-explicit data collected over 15 years in the LFDP, we address the following questions:

1. Does tropical forest subject to major hurricane disturbance exhibit landscape-level changes in community composition through time, or is there a dominant patch structure evident in the community dynamics?
2. Is the spatial scale of metastability in community composition altered by repeated, major hurricane disturbance occurring at short (relative to average) return intervals?
3. Does historical land-use affect the scaling of metastability and alter the community response to hurricane disturbance?

Methods

Study site

The study site was the 16-ha (320 × 500 m) Luquillo Forest Dynamics Plot (LFDP), located in the Luquillo Mountains of northeastern Puerto Rico (18°20′N 65°49′W; ~400 m elevation). Rainfall at the site averages 3500 mm/yr. The forest type is locally referred to as 'tabonuco forest' (after the dominant tree species *Dacryodes excelsa*) and is classified as subtropical wet forest in the Holdridge life zone system (Ewel and Whitmore 1973). The LFDP was established in 1990 shortly after Hurricane Hugo

(Thompson et al. 2002, 2004). Hurricane Hugo, a Category 4 storm at landfall (Scatena and Larsen 1991), killed 9.0% of all trees in the LFDP and caused significant damage to stems and large branches in an additional 35% (Zimmerman et al. 1994). Hurricane Georges, a Category 3 storm at landfall, struck in September 1998 and also caused widespread damage to trees throughout the Luquillo Mountains (Boose et al. 2004; Ostertag et al. 2005). While the paths of the storms differed, with the center of Hugo passing to the northeast of the site and that of Georges passing to the south, the maximum winds from the two storms were similar at our site (Canham et al. 2010). Differences in storm meteorology and the more mature condition of the forest when struck by Hugo (57 years since the previous major hurricane; Scatena and Larsen 1991) resulted in more canopy and stem damage than when the forest was struck by Georges (9 years after Hugo; Canham et al. 2010). At the plot level, and for the most common species, however, the frequency and type of damage to trees from the two storms were statistically independent (Canham et al. 2010).

The LFDP includes several areas with differing land use histories, which strongly influence present day forest composition (Thompson et al. 2002). About 1.2 ha in the northeast part of the LFDP was clear-cut for subsistence agriculture and had <20% canopy cover in aerial photographs taken in 1936. Another ~9.6 ha in the northern and central portions of the plot was used for timber harvest and some agriculture (coffee and kitchen gardens; García-Montiel 2002) and had 20–80% canopy cover in 1936. The southern 5.2 ha of the plot had >80% canopy cover in 1936 and most nearly approximates forest undisturbed by humans, although there was some selective logging as late as 1953 (Thompson et al. 2002). For the purposes of this study, we combined the different areas of secondary forest (total 10.8 ha) in the northern portion of the plot and contrasted this with the remaining (5.2 ha) relatively undisturbed southern portion.

Field methods

Following Hurricane Hugo, we made an initial survey of all dead trees dead ≥10 cm dbh (diameter at breast height, 1.3 m above ground) during September 1990 to February 1991 (Zimmerman et al. 1994). Tagging

and mapping of live trees ≥10 cm dbh was completed between June 1990 and January 1992. The initial survey of dead trees and the full census of live trees ≥10 cm dbh enabled us to determine the composition of trees ≥10 cm dbh in the LFDP at the time of Hurricane Hugo (Thompson et al. 2002). Between June 1992 and February 1994, we completed a survey of trees 1 to <10 cm dbh. Thus, initial surveys of the overstory and understory represent different times (Table 1) with respect to Hurricane Hugo. Following the initial surveys and beginning in the years 1995, 2000 and 2005, we censused all free-standing, woody stems (shrubs and trees) ≥1.0 cm dbh in the entire LFDP concurrently. We identified each individual to species (Liogier 1985), measured its dbh, marked it with a numbered tag, and recorded either the 5 × 5 m subplot in which it was located, but more often the precise location within the subplot (depending upon which census). Thus, we have a spatially-referenced record of survival, mortality, diameter-class distribution, and population size of all tree and shrub species on the 16-ha plot.

Analyses

Boose et al. (1994, 2004) described patterns of hurricane damage to vegetation at broader scales typically associated with landscape-scale studies. For the purposes of this study, plotwise analyses of community dynamics represent the landscape scale. Our goal was to determine the dominant patch size at which the scale of community dynamics was at landscape equilibrium or metastable. We used the LFDP over the three measurement intervals (Table 1) from 1989 (pre-Hugo)–1995, 1995–2000, 2000–2005 for trees ≥10.0 cm dbh and from 1992 to 1995,

1995–2000 and 2000–2005 for trees and shrubs 1 to <10 cm dbh. The 16-ha plot was divided into square quadrats ranging in size from 10 × 10 m (0.01 ha, 1600 quadrats) up to 100 × 100 m (1 ha, 16 quadrats) and we compared changes in species composition from one census to the next in quadrats of increasing area using the Morisita–Horn index of dissimilarity. This index uses information on differences in the abundance of each species, as well as overall changes in the species present in a quadrat. Unlike many similarity indices commonly used in ecology, the Morisita–Horn index is not affected by differences in quadrat size, tree density, or species richness (Magurran 2004).

For each census interval, the Morisita–Horn similarity index was computed separately for each quadrat of a given size using the abundances of species in the quadrat at time the start and end of the census interval, and then taking the mean over all quadrats of that quadrat size class. Ninety-five percent confidence intervals around the means were calculated using standard bootstrapping techniques. We plotted community dissimilarity over time as a function of quadrat size to examine the change in average community dissimilarity with increasing area sampled. For this study, we focused on short-term changes in forest composition, utilizing the 3–5 year intervals provided by the censuses of the LFDP. The census intervals represent post hurricane thinning (1992–1995, 2000–2005) and building phases (1995–2000) for this highly dynamic (1 to <10 cm dbh) small tree and shrub portion of the community. Species without secondary growth such as palms were assigned to the two size categories by separating individuals into two height categories, those with and without a trunk at 130 cm.

Table 1 Summary values of the number of individual trees and the number of species recorded on the Luquillo Forest Dynamics Plot (16 ha) in two sizes classes, 1 to <10 cm dbh and ≥10 cm dbh

	No. of individuals			No. of species		
	≥10 cm dbh	<10 cm dbh	Total	≥10 cm dbh	<10 cm dbh	Total
1989	16873			95		
1992		72378	89251*		143	155*
1995	16680	53422	70102	91	137	146
2000	17395	44599	61994	88	133	139
2005	17129	24312	41441	88	120	128

*These totals reflect all individuals and species enumerated through the 1992 census

Visual inspection of the graphics revealed that community dissimilarity typically decreased as a function of quadrat size as:

$$DISSIM = a \cdot QUADSIZE^b.$$

Log-transforming both variables results in the linear equation:

$$\log(DISSIM) = \log(a) + b \cdot QUADSIZE.$$

Thus, using simple linear regression, we tested for a significant relationship between the mean change in community composition over time and the area of the quadrat size sampled, and determined values of the intercept (a) and the rate of change in community dissimilarity with quadrat size (b) that describes the relationship.

To compare the spatial scaling of community change among different census intervals (e.g., with and without hurricane disturbance) and different tree size classes (1 to <10 cm dbh and ≥10 cm dbh), we determined the point of metastability for each interval and size class. Because community dissimilarity declined with increasing quadrat area at a constant rate, the curves had no true inflection points. Therefore, we calculated the point of maximum curvature after first scaling x and y values to range from 0 to 1, similar to the method described in Gipple and Stewardson (1998). The curvature, k, can be written as:

$$k = \frac{ab(b-1) * x^{b-2}}{\left(1 + (abx^{b-1})^2\right)^{\frac{3}{2}}}$$

where a and b are the coefficients from the equations above, and x is the quadrat size. To estimate the point of maximum curvature, we maximized k with respect to x. The quadrat size at which the curvature was maximized was then interpreted as the point of community metastability.

To test whether historical land-use influenced the magnitude of change and the spatial scale of stability in community composition following disturbance, we determined the point of metastability using the methods described above for each of the two different land use history categories. The northern 2/3rds of the LFDP, which had been clear-cut and used for agriculture, was considered to have a high-intensity land use history and the southern 1/3rd of the LFDP, which had been subject only to selective logging and

had >80% canopy cover in 1936, was considered to have a low-intensity land use history.

To determine whether the spatial scaling of community change was related to the spatial scale of hurricane damage, we quantified the basal area (BA) of trees ≥10 cm dbh that died between census intervals in each land use category as a measure of structural damage in the plot. These large trees should, for the most part, represent patterns of tree mortality caused directly by the hurricanes and other factors. We then calculated the proportion of total basal area that died in each quadrat, using the same range of quadrat sizes as for the dissimilarity calculations (0.01–1 ha), and repeated the analyses described above to determine the spatial scaling and metastability point of structural damage.

Results

Whole plot dynamics

Despite damage from two major hurricanes, plot level changes in tree abundance, species richness, (Table 1) and species composition (Fig. 1) showed remarkable stability, particularly among trees ≥10 cm dbh. Trees 1 to <10 cm dbh declined in abundance and species richness through the three census periods (Table 1) and many individual species exhibited significant declines (>50% abundance) during hurricane free census intervals from 1992 to 1995 and again from 2000 to 2005 (Fig. 1; Table S1).

All species that showed a significant change in abundance between censuses (Fig. 1) were pioneer or mid-successional tree species, or small trees and shrubs. In contrast, the abundances of late successional tree species were remarkably stable over time, even in census intervals in which hurricanes occurred. Among trees ≥10 cm dbh, between 1989 and 1995 Hurricane Hugo caused significant losses of *Casearia arborea* (CASARB in Fig. 1), several other mid-successional species, and the pioneer *Miconia tetrandra* (MICTET). During this period there were also very large increases in the abundances of the pioneer tree *Cecropia schreberiana* (CECSCH) and the tree fern *Cyathea arborea* (CYAARB; Fig. 1a). Between 1995 and 2000, which included disturbance by Hurricane Georges, there were additional losses of ≥10 cm dbh mid-successional species such as
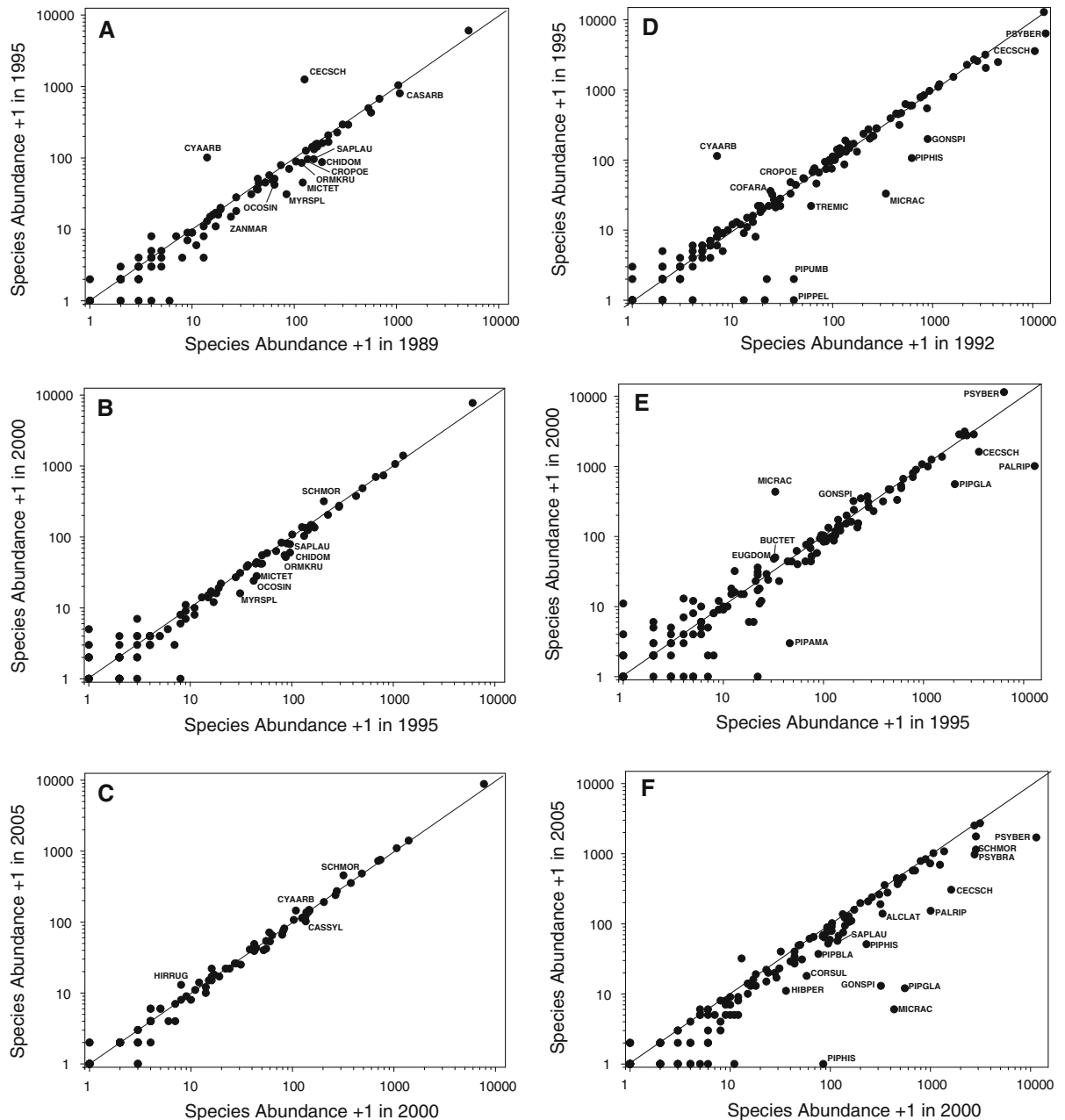
Fig. 1 Differences in species abundance between censuses of the LFDP. Diagonal lines show the 1:1 relationship (i.e., no change) in species abundance. **a** 1989–1995; ≥10 cm dbh. **b** 1995–2000; ≥10 cm dbh. **c** 2000–2005; ≥10 cm dbh. **d** 1992–1995; 1 to <10 cm dbh. **e** 1995–2000; 1 to <10 cm dbh. **f** 2000–2005; 1 to <10 cm dbh. Species codes (see text and below; also Table S1) indicate which species exhibited the largest changes between censuses. For trees ≥10 cm dbh, species were labeled if they showed a greater than 25% increase or decrease between censuses and their abundance in at least one census was >1 individual per hectare. For species 1 to <10 cm dbh, labels are provided if they showed a greater

than 50% increase or decrease between censuses and their abundance in at least one census was >2 individuals per hectare. Species and codes not mentioned in text: *Alchornea latifolia* (ALCLAT), *Buchenavia tetraphylla* (BUCTET), *Cordia sulcata* (CORSUL), *Eugenia domingensis* (EUGDOM), *Gonzalagunia spicata* (GONSPI), *Hibiscus pernambucensis* (HIBPER), *Miconia racemosa* (MICRAC), *Myrcia splendens* (MYRSPL), *Piper amalgo* (PIPAMA), *P. blattarum* (PIPBLA), *P. glabrescens* (PIPGLA), *P. hispidum* (PIPHIS), *P. peletata* (PIPPEL), *P. umbellata* (PPIPUMB), *Psychotria bracheata* (PSYBRA), *Trema micrantha* (TREMIC), and *Zanthoxylum martinicense* (ZANMAR)

Chionanthus domingensis (CHIDOM), *Ormosia krugii* (ORMKRU), *Ocotea sintinisii* (OCOSIN), *Sapium laurocerasus* (SAPLAU), and the pioneer *M. tetrandra* (Fig. 1b). In contrast, during this same period (1995–2000) the pioneer *Schefflera morototoni* (SCHMOR) increased in abundance, but there were no large increases in *C. schreberiana* or *Cy. arborea* as that observed in the post Hurricane Hugo census period 1989–1995. During 2000–2005, during which no severe hurricanes occurred, for trees ≥10 cm dbh there were large net gains in *S. morototoni*, *Cy. arborea*, and the small tree *Hirtella rugosa* (HIRRUG), and a substantial decline in the mid-sucesssional species *Casearia sylvestris* (CASSYL; Fig. 1c).

Among stems 1 to <10 cm dbh, during the period 1992–1995, there were large net gains in *Cy. arborea*, coffee (*Coffea arabica*; COFARA), and mid-successional *Croton poecilanthus* (CROPOE; Fig. 1d). During the same period, there were substantial losses in the pioneer trees *C. schreberiana* and *Trema micrantha* (TREMIC), and the small tree *Psychotria bertereona* (PSYBER), in addition to five other species of shrubs. Many of these same species showed large changes in numbers 1995–2000, not necessarily in the same direction as from 1992 to 1995. A large number of pioneer tree species, small trees, and shrubs exhibited large and significant declines in the hurricane free period of 2000–2005 (Fig. 1e, f; Table S1).

Patterns of community dissimilarity between censuses exhibited an apparent patch structure (Fig. 2), with significant curve fits in all cases (Table S2). As predicted, community dissimilarity decreased with increasing quadrat size. The curve fits for the relationship between dissimilarity and quadrat size were good for trees ≥10 cm dbh ($R^2 = 95$–98%) and suggested an average patch size of community change, or metastability point, of 0.10 ha (Fig. 2a; Table S2). A patch structure was also evident among the smaller class of trees ($R^2 = 54$–73%) and indicated an average patch size in the understory that was small and variable, ranging from 0.016 to 0.054 ha. Asymptotic values of dissimilarity approached whole plot (16 ha) community dissimilarity values for large, but not for small trees (Fig. 2). Whole plot dissimilarity was greater than the apparent asymptote for small trees and shrubs for the periods 1995–2000 and 2000–2005, indicating landscape-scale changes in community composition had occurred, in addition to those which occurred at smaller spatial scales.
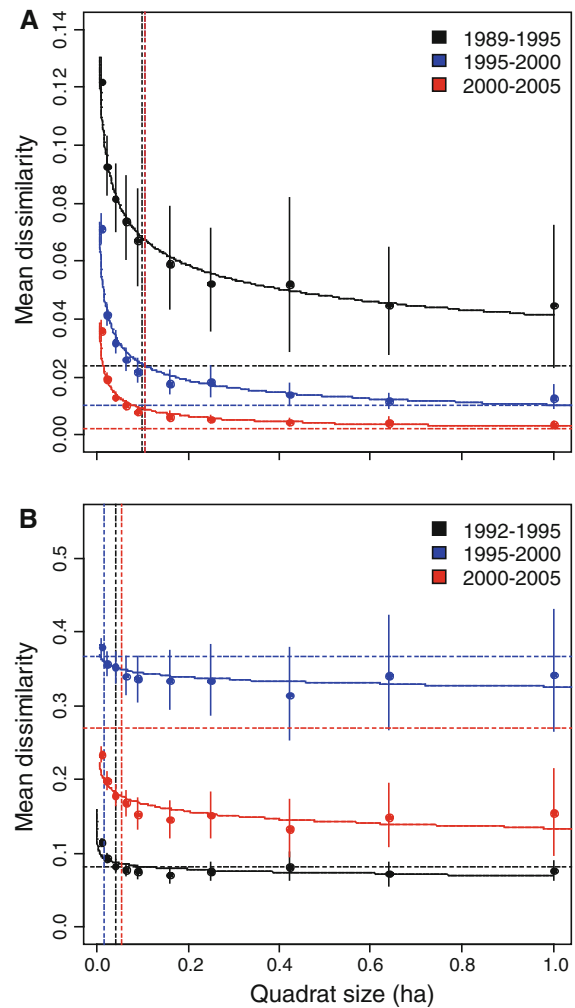

Fig. 2 Changes in community dissimilarity (Horn-Morisita index) as a function of quadrat size. **a** Trees ≥10 cm dbh. **b** Trees 1 to <10 cm dbh. *Horizontal* broken lines indicate whole plot values of community dissimilarity. *Vertical* broken lines indicate the estimate of patch size derived from the change in values as a function of quadrat size for each curve (Table S2)

Effects of land use history

Within land use types, patterns of community dissimilarity between censuses exhibited a patch structure similar to that seen at the whole plot level and, like the whole plot analyses, were more evident among large (≥10 cm dbh) trees than small (1 to <10 cm dbh) trees (Fig. 3). As reported above the curve fits for large trees were better ($R^2 = 86$–97%) than for small trees ($R^2 = 0$–94%) such that, among small trees, the curve fits were not significant for three of six combinations of
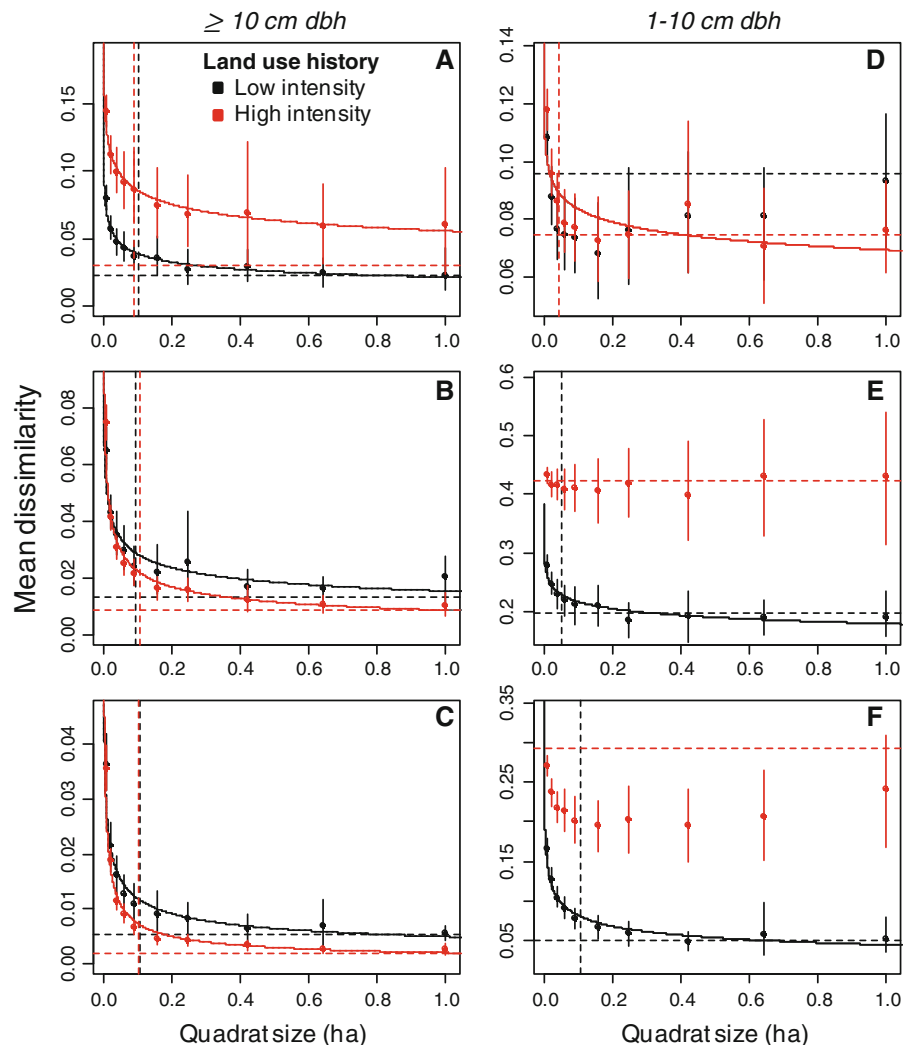
Fig. 3 Changes in community dissimilarity (Horn-Morisita index) as a function of quadrat size in areas of different land use intensities in the LFDP. **a** 1989–1995; ≥10 cm dbh. **b** 1995–2000; ≥10 cm dbh. **c** 2000–2005; ≥10 cm dbh. **d** 1992–1995; 1 to <10 cm dbh. **e** 1995–2000; 1 to <10 cm

dbh. **f** 2000–2005; 1 to <10 cm dbh. *Horizontal* broken lines indicate values of community dissimilarity for the land use area. *Vertical* broken lines indicate the estimate of patch size derived from the changes in values as a function of quadrat size (Table S2)

land use history and census interval (Fig. 3d–f; Table S2).

The patch sizes suggested by community dissimilarity patterns of trees ≥10 cm dbh were similar for the two land use types (Fig. 3a–c; Table S2) and close to the patch size, 0.10 ha, calculated for the whole plot analysis. For stems >10 cm dbh in all census periods, the decline in community dissimilarity with increasing quadrat size approached an asymptote close to the overall change in community composition obtained for the entire plot (Fig. 3a–c).

Patterns of scaling in community dissimilarity for trees 1 to <10 cm dbh were variable among land use history areas and census intervals, but two things were evident. First the absence of a significant curve fit in two cases (low land use intensity area, census interval 1992–1995 and high land use intensity area, census interval 2000–2005; Fig. 3d, f) was the result of large scale, landscape-level changes, as indicated by the increasing values of dissimilarity at larger quadrat sizes. In both of these cases, the curvature in the relationship at small quadrat sizes was similar to

those seen for the significant curves that suggested a patch size ranging between 0.046 and 0.107 ha (Table S2). There was no evidence of a patch structure at small spatial scales in the high intensity land use area in 1995–2000 (Fig. 3e). Where significant, fitted curves for the low intensity land use area did not suggest any landscape-level patch structure (Fig. 3e, f), nor did the one significant curve in the high intensity land use area (Fig. 3d). Thus, the appearance of landscape-level changes in community composition was inconsistent among land use types and census intervals.

Basal area losses due to stem mortality exhibited a significant patch structure, with mean changes suggesting a patch size between 0.024 and 0.031 ha (Fig. 4; Table S2). Close inspection, however, indicated that the curve fits were relatively poor ($R^2 = 60$–63%) because the exponential model failed to capture the initial decline in basal area, which was relatively steep in all cases. Estimated patch sizes of tree mortality were consistently greater in the area of low intensity land use (mean $= 0.031$ ha) than in the area of high intensity land use (mean $= 0.21$ ha). Most importantly, overall basal area loss was 50–100% greater in the area of high intensity land use than the area of low intensity land use over all census intervals (Fig. 4).

Discussion

In this study we address the issue of landscape patterns of hurricane disturbance from the perspective of hierarchical patch dynamics in a forest community (Turner et al. 1993; Wu and Loucks 1995) rather than from direct measurements of abiotic impacts of disturbance. Our approach allowed us to examine the overall effects of hurricanes on forest composition, including both disturbance and recovery, and to contrast patterns of community change for different tree size classes and land-use history categories. During the 15-year period of our study that included the impact of two major hurricanes and forest changes measured over three time intervals, we found that, particularly for canopy trees, the forest community exhibited a clearly identifiable point of metastability at small spatial scales near 0.1 ha. Estimated patch sizes were consistent among census intervals and between land use types and conformed
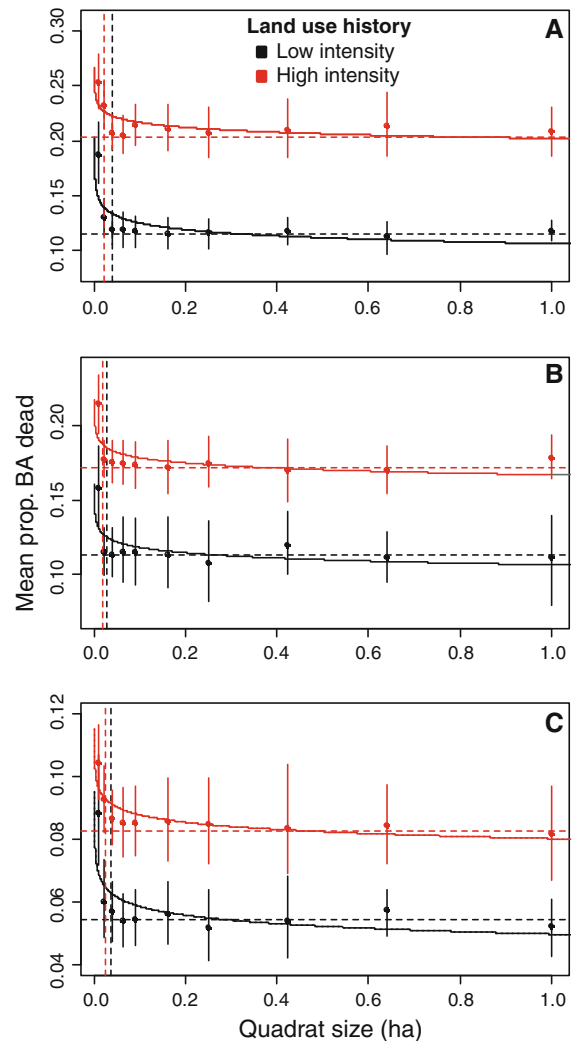

Fig. 4 Average loss of basal area (>1 cm dbh) in areas of different land use intensities in the LFDP. **a** 1989–1995. **b** 1995–2000. **c** 2000–2005. *Horizontal* broken lines indicate plot level changes in loss of basal area. *Vertical* broken lines indicate the estimate of patch size derived from the changes in values as a function of quadrat size (Table S2)

to the idea that, rather than being entirely a large scale, landscape-level disturbance, hurricane disturbance in our forested landscape is predominantly a patch driven process.

Whole plot dynamics

For canopy trees ≥ 10 cm dbh, landscape-level changes in species abundance in the LFDP largely reflected community stability in response to two severe hurricanes that occurred 9 years apart. In the

community of large trees, we see no evidence that the hurricanes established a landscape-wide trajectory of successional forest change (Turner et al. 1993) in the LFDP. The few species that did show substantial hurricane-induced stem damage and mortality (Zimmerman et al. 1994; Ogle et al. 2006; Canham et al. 2010) are species whose juveniles often recruit in high numbers following a storm (Brokaw 1998; Uriarte et al. 2004), particularly in areas where canopy damage causes high light levels in the understory (Uriarte et al. 2005; Comita et al. 2009). Mature forest species, in contrast, appear highly resistant to damage from storm winds, tolerating branch loss that reduced the likelihood of damage to the main trunk, and allowed them to regenerate a new crown rapidly (Yih et al. 1991; Zimmerman et al. 1994; Bellingham et al. 1994), thus restoring shade to the understory. Following a building phase, during which shrubs and saplings of pioneers dominate the understory, a period of thinning follows, leading to the loss of the abundant secondary forest species in the small size classes (Uriarte et al. 2004). Thus, in forests where species composition is largely unmodified by human disturbance, the life history characteristics and dominance of the community by canopy species is relatively resistant to hurricane disturbance and results in low tree mortality (<10%; Zimmerman et al. 1994) and imparts landscape-level community stability among trees ≥10 cm dbh, in spite of two episodes of major hurricane disturbance.

Spatial patterns of community change of canopy trees through time in the LFDP exhibit a point of metastability at a patch size of around 0.10 ha, which is very similar to that found at our site using studies of canopy structure (Brokaw and Grear 1991) and understory light levels (Fernández and Fetcher 1991) following Hurricane Hugo. Thus, our results confirm the existence and the similar dimension of patch disturbance caused by hurricanes found in these other studies.

While our study indicates that hurricane disturbance is a patch-driven process in the LFDP, the average size and frequency of disturbances are nonetheless very different from forests that do not experience hurricanes. The sizes of treefall gaps in other forests, which, while quite variable, nevertheless show an average size between 0.005 and 0.01 ha (reviewed in Ferreira de Lima et al. 2008), that is, one-tenth to one-twentieth the average hurricane-

caused gap size indicated in the LFDP. Estimates of the average recurrence intervals of treefalls in hurricane-free forests are also quite variable (Brokaw 1985), but suggest that recurrence intervals are longer than that experienced in the LFDP. For example, in two frequently studied forest sites free of hurricane disturbance, La Selva, Costa Rica, and Barro Colorado Island, Panama, the return interval for tree fall gaps falls in the range of 80–135 years (Hartshorn 1978; Brokaw 1982). This is greater than the average return interval of hurricanes in eastern Puerto Rico (50–60 years; Scatena and Larsen 1991). Thus, the disturbance regime in the LFDP generates treefall gaps that are much larger and occur somewhat more frequently than that in hurricane-free forests, leading to a canopy that is, on average, lower, and smoother compared to hurricane-free forests (Brokaw et al. 2004).

Effects of land use history

Our results confirm the patterns revealed elsewhere (Uriarte et al. 2009; Comita et al. in press) that the dominance of secondary species in the area of high intensity human land use in the north part of the plot leads to greater levels (50–100%) of tree mortality and canopy damage from hurricanes than in the area of low intensity land use. Here we showed that this effect extended through the hurricane quiescent interval of 2000–2005, indicating that tree turn-over, and species turn-over, in secondary forest is consistently greater than that in the more mature forest in the low intensity land use area. Despite significant differences in tree composition and diversity (Thompson et al. 2002), and contrary to our expectations, the patch sizes of community change in areas of low and high land use intensity and the whole plot were nearly identical to one another and revealed a dominant patch size of 0.1 ha.

Understory patterns of the spatial structuring of community change through time were variable and difficult to interpret in some cases. Separating the results for the understory in the two different land use histories identified, in most cases, a signature of spatial scaling in community change, but one with a dominant quadrat size that was the same or smaller than that observed for the canopy trees in the same land use area. Curve fits, however, were not always significant, usually because of the substantial amount

of community change at the largest spatial scale. A more sophisticated curve-fitting strategy would resolve this problem, but the patterns appear self-evident: there was a combination of a small patch structure seen in other census intervals combined with the signature of landscape-wide community change. Landscape-wide changes in community understory composition appeared in the low land use intensity area during 1992–1995 and in the high land use intensity area in the intervals of 1995–2000 and 2000–2005, but not in other combinations of time interval and land use type. We interpret these patterns as interactions between forest strata, as follows. There was extensive canopy damage in the high land use intensity area from Hurricane Hugo (1989) and canopy recovery was likely slower to shade the understory during the 1992–1995 census period than in 2000–2005. Meanwhile the understory community in the high land use intensity area, with its heavily damaged canopy, remained in a building phase and exhibited relatively little overall community change. In contrast, in the low land use intensity area, relatively rapid canopy closure from the recovering crowns of mature forest species caused the rapid loss of shrub and pioneers species, which resulted in landscape-scale changes in the understory community. In subsequent intervals, which included Hurricane Georges, higher average light levels in the understory (Comita et al. in press) and more rapid canopy dynamics in the high land use intensity area apparently drove landscape-scale changes in the pioneer and shrub community that determined the spatial scaling of community change. Thus, compounded effects of land use history on hurricane-induced forest dynamics evident in the understory were regulated indirectly by the impact of land use history on the composition of canopy trees (Thompson et al. 2002).

Analysis of the patch structure of basal area loss due to tree mortality on the LFDP using the methods developed here added little to the analyses of the community change of live trees through time. Curve fits to the spatial pattern of tree mortality were relatively poor and suggested a much smaller dominant patch size than that measured using the community response and in other, more direct studies of the spatial scale of hurricane disturbance (Brokaw and Grear 1991; Fernandez and Fetcher 1991). This is to be expected because basal area lost between

censuses reflects the spatial signature of individual tree deaths and does not necessarily represent canopy openings resulting from branch breakage, nor the effect on the understory caused by falling branches and trees.

Conclusions

Theory suggests that community and ecosystem response to severe disturbance should be, in terms of their spatial dynamics, qualitatively different from less severe disturbance, depending on the frequency and spatial extent of the disturbance type (Turner et al. 1993, 1998; Romme et al. 1998). This study emphasizes the fact that strong hurricanes are not a "severe" disturbance in the sense that they cause extremely high levels of tree mortality as theoretical perspectives have assumed (Freelich and Reich 1999). Although forests exposed to strong hurricane wind speeds suffer extensive canopy damage (Zimmerman et al. 1994; Canham et al. 2010), this is not extreme enough in all cases (Lugo and Scatena 1996) to obscure the pattern of patch metastability in the community dynamics in response to the disturbance. Thus, how we interpret the forest ecosystem response to wind disturbance (e.g., Romme et al. 1998; Brokaw et al. 2004) cannot simply be predicated on whether the forests are subject to disturbance from cyclonic storms, but rather, on the extent to which these disturbances have the ability to cause widespread tree mortality and, if they do not, what the resulting dominant patch size is. Contrary to our expectations, the dimension of patch metastability in the scaling of temporal community change was not altered by land use history or a recent history of hurricane disturbance. This suggests a common structural characteristic of the forest represented by the LFDP, one that does not vary with disturbance history and that underlies its spatial dynamics (Sprugel and Bormann 1981; Solé and Manrubia 1995; Muller-Landau et al. 2006; Kellner and Asner 2009). Differences in land use history, however, through effects on the composition of the canopy trees, do cause complex differences in the spatial dynamics of the understory, some of which are expressed at the landscape scale in addition to small-scale patch-level dynamics. Overall, however, our results emphasize that hurricane disturbance in this

forest has a dominant patch structure that is largely invariant with respect to past human and hurricane disturbance.

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