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Hurricane-Induced Massive Nutrient Return via Tropical Dry Forest Litterfall: Has Forest Biogeochemistry Resilience Changed?

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ABSTRACT

High-intensity hurricane disturbances have severe consequences on forest structure and functioning. Through wind force and heavy rainfall, they cause extensive canopy removal and an input of fine litter and woody debris well above normal levels. We examined litterfall *N* and *P* concentrations and fluxes before and after Hurricane Patricia (category 4) landfall in October 2015 in the seasonally dry tropical forest of the Chamela region, Jalisco, Mexico. Additionally, we compared the forest response to Patricia with those to Hurricane Jova (2011), from the Eastern North Pacific basin and to Hurricane Dean (2007) from the Atlantic basin. Nutrient concentrations in hurricane-induced litterfall in October 2015 were 2.2 times higher in leaf litter than in the woody fraction. Both litterfall *N* and *P* concentrations during the period November–February following the hurricane were generally higher than in similar periods in years previous to and after Patricia. Nutrient fluxes in October 2015 (75.9 kgN/ha and 3.6 kgP/ha) represented 55% (*N*) and 52% (*P*) of the total fluxes that year, which were much higher than those in any of the three years following the hurricane. These results suggest that forest biogeochemical resilience has changed in the short term. The annual litterfall *N* and *P* fluxes during the year of Hurricane Dean were lower than in 2011 and 2015, but similar to non-hurricane years. After Patricia, the annual *N* flux was higher, but the annual *P* flux lower than after Jova, and the former represents the largest annual *N* flux in our more than 25 years record.

Key words: litterfall; nitrogen; phosphorus; hurricane; forest resilience; nutrient fluxes.

HIGHLIGHTS

- Hurricane Patricia-induced litterfall *N* and *P* fluxes were $>$ 50% of the annual fluxes.
- The annual *N* flux in 2015 represents the largest

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value recorded over a 25-y period.

- Nutrient fluxes three years after Patricia are still lower than pre-hurricane values.

INTRODUCTION

High-intensity hurricane or cyclone disturbances have severe consequences for ecosystems and on human settlements. A recent assessment by the Intergovernmental Panel on Climate Change (IPCC) indicates that tropical hurricanes will increase in intensity due to global warming (Seneviratne and others 2021). This is particularly relevant since hurricane effects on forest structure and functioning are typically related to hurricane strength. Wind force and heavy rainfall associated with these extreme events cause extensive canopy removal and thus an input of fine litter and woody debris well above normal levels (Richardson and others 2010; Martínez-Yrízar and others 2018), although the spatial distribution of forest alteration may vary greatly across the landscape. The related observed input of higher than normal amounts of *N*, *P* and labile *C* to the soil is likely to alter decomposition rates and nutrient cycling in the short and the long terms (Scatena and others 1996; Gutiérrez del Arroyo and Silver 2018).

One key element to fully understand the consequences of such natural disturbances is to establish the level of ecosystem or forest resilience (sensu Hodgson and others 2015). According to their definition resilience includes two components: a) resistance, the ability not to change substantially in structure or function in response to disturbance, and b) recovery, the return path or trajectory to the ecosystem state prior to disturbance. Understanding ecosystem resilience is relevant not only for ecological science, but also to develop management strategies for the recovery and maintenance of biodiversity and ecosystem services. Thus, the study of ecosystem responses to hurricane physical damage is crucial for determining the forests capacity to maintain ecosystem resilience under natural disturbance regimes (Whigham and others 1991; Seidl and others 2014).

Hurricanes and typhoons have been considered frequent disturbances to ecosystem dynamics both in the Caribbean and in the Pacific oceans (Tanner and others 1991; Xu and others 2004a; Wang and others 2013; Shiels and others 2014). Several studies in these regions have documented the ecosystem biogeochemical changes after hurricanes; for example, litterfall nutrient fluxes or groundwater and stream chemistry (Lodge and others 1991; McDowell and others 1996; Herbert and others 1999; Lin and others 2003; Xu and others 2004a; Van Bloem and others 2005; Lin and others 2011; Wang and others 2013; McDowell and Liptzin 2014; Silver and others 2014). In the case of Mexico, much of our knowledge about hurricane-induced structural changes on ecosystems derived from studies on the Atlantic coast and the Gulf of Mexico (Whigham and others 1991; Gutiérrez-Granados and others 2011; Vandecar and others 2011). Recently, studies conducted in the Western Pacific Coast (Álvarez-Yépiz and others 2018) have complemented our understanding. However, studies analyzing the functional or biogeochemical perspectives of hurricane effects and ecosystem recovery are scant. A deeper understanding of the ecological consequences of hurricane disturbance should aid the definition of better management strategies to reduce vulnerability of coastal tropical ecosystems in Mexico.

Information on hurricane landing frequency in the Pacific coast of Mexico indicates the landfall of ten major hurricanes (category ≥ 3) between 1949 and 2006 (Blake and others 2009). Recently, two of them made landfall in the Chamela-Cuixmala region in the state of Jalisco: Hurricane Jova (category 2) in 2011 and just four years later, the stronger, potentially catastrophic category 4 Hurricane Patricia (Álvarez-Yépiz and others 2018). This was considered the strongest hurricane on record in the Eastern North Pacific and North Atlantic basins (Kimberlain and others 2016). Jova and Patricia significantly increased the hydroclimatic variability in this region, which is characterized by highly variable intra- and interannual rainfall (Maass and others 2018).

Long-term research has improved our understanding of ecological processes in a wide range of ecosystems and encompassing a variety of topics, such as the biogeochemical links between forests and stream ecosystems, the maintenance of species diversity in tropical forests and the relationship with ecosystem functioning in temperate grasslands, among many others (Likens 2004; Hughes and others 2017). Moreover, long-term monitoring of ecosystem structure and functioning has made possible the detection and analysis of infrequent events or disturbances that may produce long-term ecological changes (Turner and others 2003; Gaiser and others 2020). Thus, a baseline prior to a natural disturbance, in our case hurricanes, has been proposed as a needed reference to document the degradation or recovery of ecosystem functions following disturbance (Kotiaho and others 2016), and to avoid confounding factors in the interpretation of storm effects (Heartsill-Scalley and López-Marrero 2021). In the tropical dry forest (TDF) in Chamela, Jalisco, Mexico, our long-term research project spanning four decades, has allowed us to determine the extent of rainfall and runoff variability (Maass and others 2018), the canopy recovery process (Parker and others 2018) and primary productivity changes (Martínez-Yrízar and others 2018) in response to the Jova and Patricia hurricanes. Biogeochemical processes were documented in response to Jova (Jaramillo and others 2018), but not to disturbance from Patricia. Although these extreme events share many similarities regarding their immediate visible effects on vegetation, quantification of the individual events is relevant to properly assess the forest's susceptibility to future hurricane-related damage and the legacy effects on forest biogeochemistry.

In this study, we focus on litterfall nitrogen (*N*) and phosphorus (*P*) dynamics before and after Hurricane Patricia to establish how litterfall concentrations and fluxes of these two key elements responded to an intense and rare hydrometeorological disturbance. Additionally, using our long-term data, we examine forest biogeochemical resilience by comparing forest response between the two Pacific hurricanes and that from Hurricane Dean, originated in the Atlantic basin four years prior to Jova, but similarly with ecosystem consequences in the Chamela TDF (Maass and others 2018). Based on the litterfall mass response to Jova and Patricia hurricanes (Martínez-Yrízar and others 2018), we expected that litterfall *N* and *P* transfer to the forest floor after the stronger Patricia storm would exceed that from Jova. A recent study at Chamela (Parker and others 2018) documented that ecosystem characteristics such as canopy structure, height, the gap fraction and aboveground biomass, all heavily affected by Hurricane Patricia, are recovering at different rates and that the time scales for some processes may require decades to recover even in the absence of other natural disturbances. Given these findings, we hypothesized that forest biogeochemical processes, specifically litterfall nutrient cycling, would also show diminished resilience (that is, resistance and recovery) after the Patricia storm, especially when compared to the forest response after Hurricane Jova in 2011. This is expected considering the infrequent exposure of the Chamela TDF to the direct effects of repeated hurricane landfall, in contrast to subtropical forests experiencing recurrent typhoons (Lin and others 2003; Xu and others 2004a).

MATERIALS AND METHODS

Study area

The study was conducted at the long-term ecological research site in the Chamela-Cuixmala Biosphere Reserve (hereafter, Chamela), in the Pacific coast of Mexico (19º29′N; 105º03′W). The landscape is dominated by low hills (< 300 m elevation) with steep slopes (> 20º) (Cotler and others 2002). Soils are young, shallow (0.5–1 m depth), predominantly sandy loams, and classified as Typic Ustorthents (USDA system). Average annual temperature is 25.6 °C (1980–2018) with small fluctuations among years (standard deviation of 3.4 °C). Monthly mean minimum and maximum temperatures are 16.4 °C (March) and 32.6 °C (August), respectively. Mean annual rainfall is 800.4 mm (1983–2018), highly seasonal, with 87% falling between June and October, and September as the wettest month on average (212 mm; data from the meteorological station at Chamela, IBUNAM and the ''Watershed Project,'' UNAM). Annual rainfall (June to the following May) is highly variable (range from 334 to 1,506 mm), which contrasts with the small variation in mean annual temperature. Only 6% of rainfall events are greater than 50 mm, but these events, associated with hurricane activity in the Pacific, deliver 42% of the total precipitation to the area (Maass and Burgos 2011; Maass and others 2018).

The dominant vegetation is a highly diverse undisturbed tropical dry forest (1,149 vascular plants), with trees 4–15 m tall and a well-developed understory (Lott and Atkinson 2002). Forest phenology is markedly seasonal. Leaves are produced at the beginning of the rainy season (July) and may remain until senescence at the end of the growing season (October–November) if unperturbed by storms or by herbivore damage (Rentería and others 2005). Most species are deciduous and remain leafless during the dry season (November–June) each year (Bullock and Solís-Magallanes 1990; Martínez-Yrízar and others 2018), but many may produce a second flush of leaves in response to unexpected out-of-season rainfall (Bullock and Solís-Magallanes 1990).

Annual litter production (1987–2010, non-hurricane years) varies between 332 ± 27 and 517 ± 21 g/m^2 (mean ± 1SE) and monthly litterfall from a minimum of 22.7 ± 2.8 (May) to a maximum of 51.6 ± 2.1 g/m^2 (December; mean ± 1SE). The period of maximum litterfall, typically between November and February of the phenological year (Anaya and others 2012; Martínez-Yrízar and others 2018), also represents a period for maximum nutrient flux from the vegetation to the forest floor (Jaramillo and Sanford 1995; Campo and others 2001).

Lott (2002) lists 227 tree species within the Chamela-Cuixmala Reserve, 23% of which belong to Fabaceae, the most important family and with many species ranking high in abundance (Durán and others 2002). This results in a high number of potentially *N*-fixing plant species, several showing nodule activity in the field (González-Ruiz and others 2008), and in high ecosystem *N* stocks (Jaramillo and others 2003). Both, leaf and litterfall *N* and *P* concentrations in the Chamela TDF are high when compared to those in other seasonally dry tropical forests (Jaramillo and Sanford 1995; Jaramillo and others 2011).

Field design

Five small watersheds (12–28 ha each) have been gauged for long-term ecological research since 1981 in Chamela (Sarukhán and Maass 1990; Maass and others 2018). One 2,400 m^2 permanent plot (80 × 30 m) was established at the middle position in each watershed, with its long axis perpendicular to the stream channel and covering both slopes (generally North- and South-facing slopes). Thus, each slope includes a 1200 m^2 (40 × 30 m) subplot divided into 10 × 10 m quadrats (Martínez-Yrízar and others 2018).

Litterfall sampling

Litterfall has been collected monthly, since 1982, during the dry season and bi-weekly during the rainy season, using conical fiberglass mesh traps (1.4 mm mesh size), 50 cm in diameter and 50 cm deep, supported by three 1 m tall aluminum stakes fixed into the ground, as fully described in Martínez-Yrízar and others (2018). Briefly, it comprises 24 litter traps per plot (one per 10 × 10 m quadrat), that is 12 traps on each slope of the watersheds. Litterfall samples consisted of all fine dead plant material (that is, leaves, reproductive structures, and small woody debris ≤ 1 cm in diameter) accumulated in the litter traps. Dead branches greater than 1 cm in diameter were discarded. The samples were dried at 80° C for 72 h and weighed. In this study, we included samples collected between July 2013 and June 2019. These represent six phenological years, each starting in July (the month of the rainy-season leaf flush) of a given year to June of the following year when most trees are leafless (Anaya and others 2012).

To quantify the hurricane effect on litterfall components, six randomly chosen litter traps per plot were each sorted out into foliar and non-foliar material for the October 2015 collection (two weeks after Hurricane Patricia landfall), similar to the procedure used with Hurricane Jova for the October 2011 litterfall samples (Jaramillo and others 2018). These components are referred to as leaf (blades, petioles, raquises, and reproductive structures) and woody (all branches ≤ 1 cm in diameter) litterfall fractions. All samples were dried at 80° C for 72 h and weighed.

Chemical analyses

Nitrogen and *P* concentrations in litterfall samples (that is, all fine dead material) were determined monthly during the phenological year of Hurricane Patricia landfall (July 2015 to June 2016). In addition, *N* and *P* were determined separately for the leaf and woody fractions of October 2015, the month of hurricane landfall. Their weighted means were estimated to compare with the litterfall nutrient concentrations from the non-hurricane months of this phenological year. The number of monthly litterfall samples for *N* and *P* determinations in non-hurricane years (2013–2014 and 2016–2018), a total of 24 per plot, was reduced to six per plot per month by pooling the plant material of four adjacent traps. The monthly samples were then pooled by four-month periods in each phenological year: the rainfall period (July–October), when the canopy is fully green, the wet-dry transition period (November–February), when most of the leaves drop, and the dry period (March–June), when the forest is leafless. Thus, we determined *N* and *P* concentrations in 18 composite litterfall samples per plot per year (6 samples per plot and period × 3 periods), in each of the five watersheds (a total of 90 samples per phenological year). Litterfall samples were ground in a mill to pass a 40-mesh screen. Total *N* and *P*, concentrations (expressed as mg/g), were determined colorimetrically with an autoanalyzer after acid digestion by a semi-Kjeldahl method (Bran-Luebbe AutoAnalyzer III, Norderstedt, Germany; method No. 696-82 W; Technicon Industrial Systems 1977). Total *P* was determined by the molybdate method after ascorbic acid reduction (Murphy and Riley 1962). Nitrogen and *P* fluxes (kg/ha) were calculated by multiplying nutrient concentrations by the corresponding litterfall dry masses.

Statistical analyses

To determine the effect of Hurricane Patricia on the monthly nutrient concentrations we fitted linear mixed effects models. The models included month as a fixed effect, a random effect of sample nested within plots, and a term to account for unequal variances among plots. A posteriori tests involved mean comparisons by Tukey HSD. Models were fitted with the ''lme'' function in the ''nlme'' package for R.

To examine litterfall *N* and *P* concentrations in the transition periods (November–February), *N* and *P* fluxes during the rainy periods (July–October) and phenological-year total *N* and *P* fluxes, in years prior to and after hurricane disturbance, we performed one-way analysis of variance (ANOVA) followed by Tukey HSD tests. Variables were log-transformed to satisfy homogeneity of variance assumptions when needed, but results are shown in their original scale of measurement. Differences among months, periods or years were declared statistically significant at $p < 0.05$. ANOVA was performed with SPSS v. 20. In all cases, sample size is five replicate plots, one within each watershed.

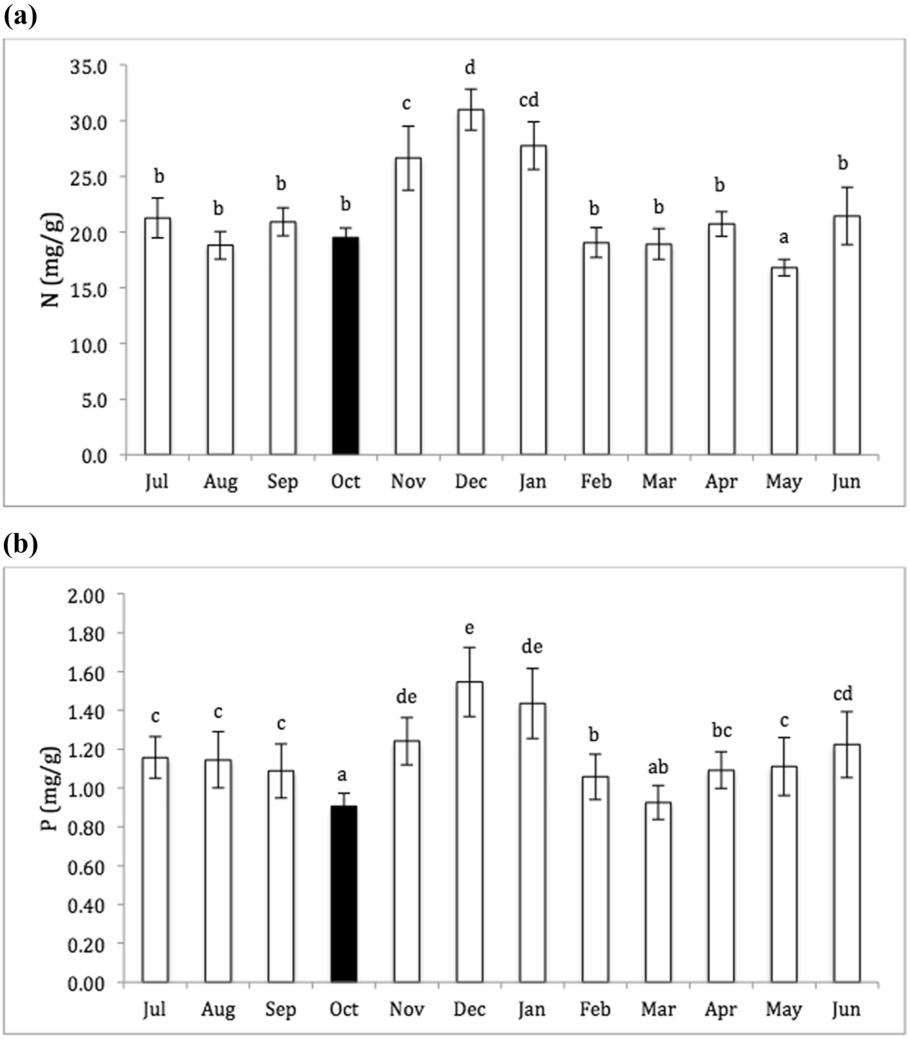

Figure 1. Litterfall monthly nitrogen **a** and phosphorus **b** concentrations during the 2015 phenological year (July 2015–June 2016) in the tropical dry forest in Chamela, Jalisco, Mexico. The dark bar indicates the month of Hurricane Patricia landfall. Each bar represents the mean (± 1SE) of five long-term monitoring plots, one per watershed. Bars with no common letters are significantly different at $p < 0.05$ according to Tukey HSD test.

Results

Nutrient concentrations in hurricane-induced litterfall components (that is, leaves and woody fractions) in October 2015 were 2.2 times higher in leaf litter ($N = 24 \pm 2$ mg/g; $P = 1.12 \pm 0.17$ mg/g; mean and SE) than in the woody fraction ($N = 10.7 \pm 1.5$ mg/g; $P = 0.49 \pm 0.13$ mg/g). The monthly comparisons during the phenological year of Hurricane Patricia showed that the highest litterfall *N* and *P* concentrations occurred between November and January, two to three months after hurricane landfall, with both *N* and *P* peaking in December (Figure 1a, b). Pooling the litterfall samples by season (rainy, transition and dry) showed that *N* and *P* concentrations during the rainy season (July–October) of 2015 were similar or lower than in the rainy season in years without hurricane disturbance (Figure 2a, b). In contrast, litterfall *N* concentrations during the transition period (November–February) following the hurricane were higher than in transition periods in years previous to and after Patricia (Figure 2a). Although *P* concentrations in the transition period after the hurricane were high, these were similarly high in other years (for example, 2018; Figure 2b).

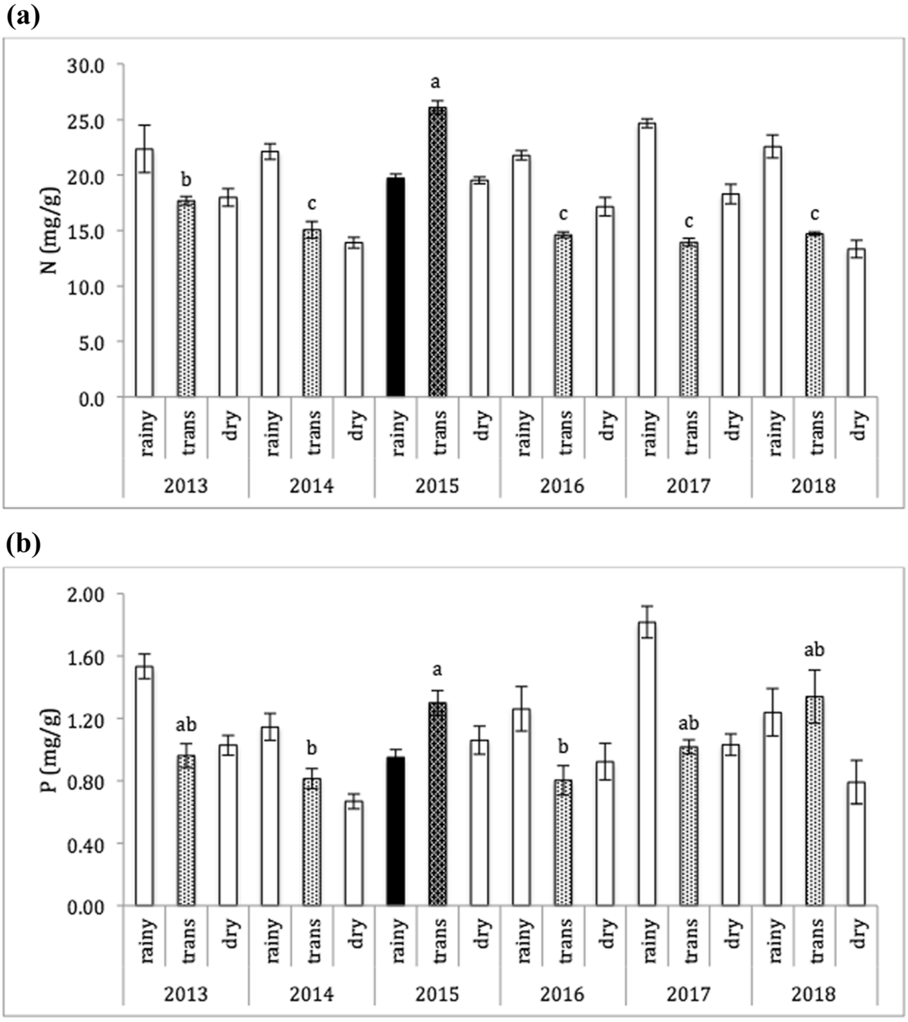

Figure 2. Litterfall nitrogen **a** and phosphorus **b** concentrations (mg/g) in years previous to and after Hurricane Patricia in the tropical dry forest in Chamela, Jalisco, Mexico. Each bar represents the mean (± 1SE) of five long-term monitoring plots, one per watershed. Rainy = rainy period (July to October); trans = transition period (November to February); dry = dry period (March to June). The year number indicates the start of the phenological year in July to June of the following year. The dark bar denotes the period for Hurricane Patricia landfall; the stippled bars show the transition periods. Dark stipple identifies the transition period after Hurricane Patricia landfall. ANOVAs for log-*N* and log-*P* concentrations in the transition periods were statistically significant at $p < 0.01$. Bars with no common letters are significantly different at $p < 0.05$ after a Tukey HSD test.

Table 1. Nitrogen and Phosphorus Fluxes (kg/ha) in the Phenological Year (July 2015 to June 2016) of Hurricane Patricia Landfall in the Tropical Dry Forest of Chamela, Jalisco, Mexico

	Nitrogen (kg/ha)	Phosphorus (kg/ha)
Leaf (October)	60.9 (2.8)	2.8 (0.2)
Woody (October)	14.7 (2.0)	0.7 (0.1)
Total October	75.9 (4.0)	3.6 (0.3)
Mean pre-Patricia (July–September)	7.8 (0.7)	0.4 (0.1)
Mean post-Patricia (November–June)	4.9 (0.6)	0.3 (0.03)
Total (July 2015 to June 2016)	138.3 (7.7)	6.9 (0.6)

Fluxes are shown for each litterfall fraction (leaf and woody) and the October total, as well as monthly mean values prior and after the hurricane landfall (October). Total fluxes in 2015 represent the mean of five long-term monitoring plots, one per watershed. Values in parentheses are 1SE.

Hurricane-induced litterfall nutrient fluxes in October 2015 were much greater via the leaf than the woody fraction (Table 1), each adding to a total of 75.9 kgN/ha and 3.6 kgP/ha. These fluxes were much higher than any other month previous to and after the hurricane (Table 1) and represented 55% (*N*) and 52% (*P*) of the total *N* and *P* fluxes of the 2015 phenological year. When the monthly data were summed up according to season (rainy, transition and dry), rainy-season *N* and *P* fluxes in 2015 were, as expected, much greater than the fluxes of any other rainy-season in the phenological years prior to and after Patricia (Figure 3a, b). The 2015 *N* flux, but not the *P* flux, was higher when compared to the two phenological years (2013 and 2014) previous to the hurricane (Figure 4a, b), which were also very humid, with annual precipitation 1.3 and 1.9 times higher than average, respectively. In contrast, both *N* and *P* fluxes were much higher than the mean fluxes from the three phenological years following the hurricane, which represented 48% (*N*) and 58% (*P*) of those in 2015, but 64% (*N*) and 69% (*P*) of the mean fluxes prior to the hurricane (2013–2014).

DISCUSSION

The unprecedented hydrometeorological variability in the Chamela region associated with the landfall of the category 2 Hurricane Jova followed four years later by the category 4 Hurricane Patricia represented a unique sequence of extreme events to test TDF biogeochemical resilience (sensu Hodgson and others 2015) to repeated natural disturbance. Similar to our study, a sequence of two hurricanes, although spaced several more years apart, was also used to describe tropical forest post-disturbance trajectories in Puerto Rico (Ostertag and others 2003). Here, we used litterfall nutrients to assess the forest biogeochemical response to Hurricane Patricia at three temporal scales: immediate (days after the event), early (one to several months after the event) and short term (up to three years after the event). The immediate effects were evident in the remarkable increase in the magnitudes of the litterfall *N* and *P* fluxes in October 2015, which corresponded to 50% of the annual 2015 fluxes, but up to 77% (*N*) and 62% (*P*) of annual fluxes of generally wet, non-hurricane years (2010, 2012, 2013, 2014) previous to 2015. Such fluxes represent a massive return of organic matter and nutrients to the forest soil in the interval of only a few days. Their magnitude greatly exceeds, for example, *N* and *P* return in subtropical dry forest of Guánica, Puerto Rico (Van Bloem and others 2005) and in subtropical broad-leaved forest in Japan (Xu and others 2004a) after cyclonic disturbances, respectively. They are, however, significantly smaller than corresponding inputs in subtropical wet forest affected by hurricanes (Lodge and others 1991; Ostertag and others 2003). When the October 2015 *N* and *P* fluxes are summed to those of the other rainy-season months (July–September), together they greatly exceeded the rainy-season fluxes in years before and after the year of Patricia, regardless of rainfall amount. In our view, this highlights the relevance of hurricane winds strength, in agreement with Van Bloem and others (2005), triggering massive leaf and branch fall, and thus, the transfer of nutrients to the soil well above normal levels.

The significant *N* and *P* fluxes from litterfall in tropical and subtropical forests, wet and dry, frequently exposed to strong hurricanes or typhoons (Lodge and others 1991; Whigham and others 1991; Herbert and others 1999; Lin and others 2003; Xu and others 2004a; Van Bloem and others 2005; Wang and others 2013) have been attributed to either increased nutrient concentrations in litterfall after hurricane impact (Whigham and others 1991), to leaf-fall occurring prior to nutrient

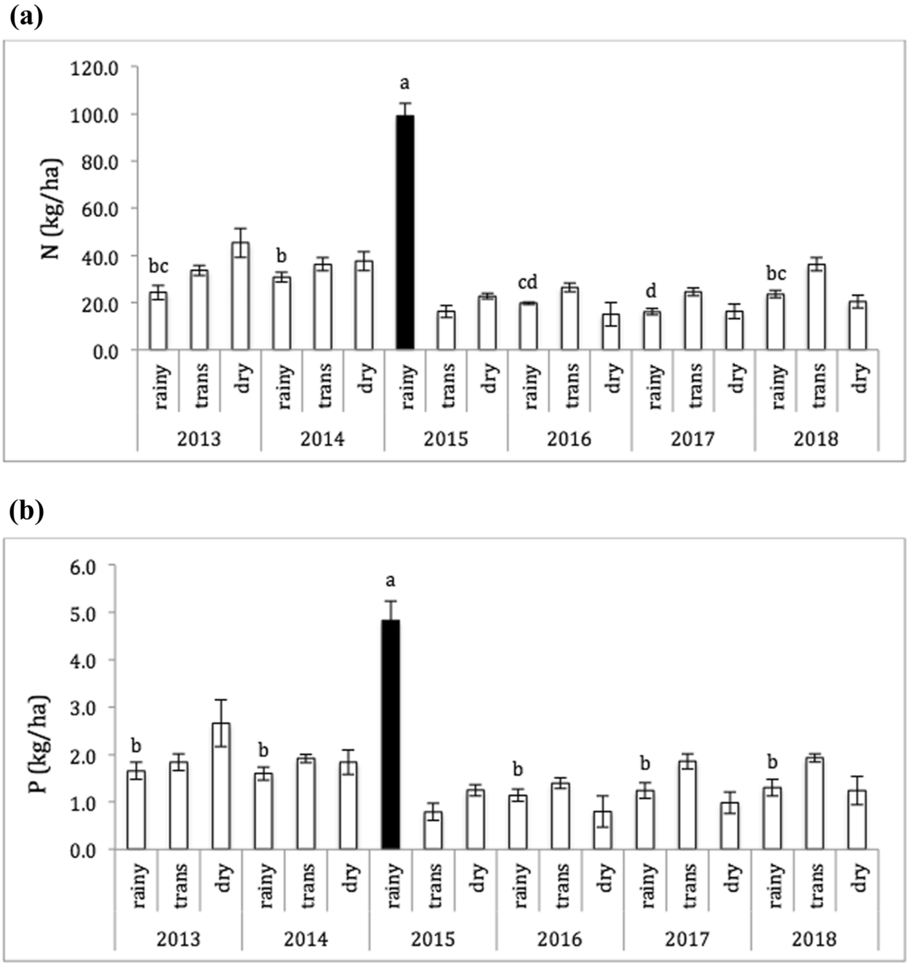

Figure 3. Litterfall nitrogen **a** and phosphorus **b** fluxes (kg/ha) in the phenological years previous to and after Hurricane Patricia in the tropical dry forest in Chamela, Jalisco, Mexico. Each bar represents the mean (± 1SE) of five long-term monitoring plots, one per watershed. Rainy = rainy period (July to October); trans = transition period (November to February); dry = dry period (March to June). The year number indicates the start of the phenological year in July to June of the following year. The dark bar denotes the period for Hurricane Patricia landfall. ANOVAs for log-*N* and *P* fluxes in the rainy periods were statistically significant at $p < 0.001$. Bars with no common letters are significantly different at $p < 0.05$ after a Tukey HSD test.

resorption or retranslocation (Lodge and others 1991; Van Bloem and others 2005; Wang and others 2013) or to diminished retranslocation in leaves produced after a typhoon (Xu and others 2004b). Interestingly, in our study, nutrient concentrations in litterfall were not higher during the hurricane month than in months prior to or after the storm disturbance.

The immediate effects (October 2015) of Hurricane Patricia on litterfall nutrients differed from those of the October 2011 category 2 Hurricane Jova (Jaramillo and others 2018). The total leaf- and woody-fraction fluxes during Patricia were 1.9 (*N*) and 1.7 (*P*) times greater than those from Jova. This was expected from the litterfall mass response, which was 1.9 times greater after Patricia than after Jova (Martínez-Yrízar and others 2018). In contrast, nutrient concentrations were quite similar between the two events (Jaramillo and others 2018; this study). Examination of each fraction's contribution independently shows that leaf *N* and *P* fluxes largely explained such differences, since they were 2.2 (*N*) and 1.9 (*P*) times those resulting from Jova. This is likely a consequence of the synergistic effect of high rainfall amount accompanied by stronger wind-force associated with category 4 Hurricane Patricia when compared to category 2 Jova (maximum wind speed, 201 km h^{-1} Jova and 322 km h^{-1} Patricia; precipitation, 187.9 mm Jova and 142.6 mm, Patricia; Parker and others 2018). The high hurricane rainfall intensity (Maass and others 2018), the high litterfall mass and nutrients

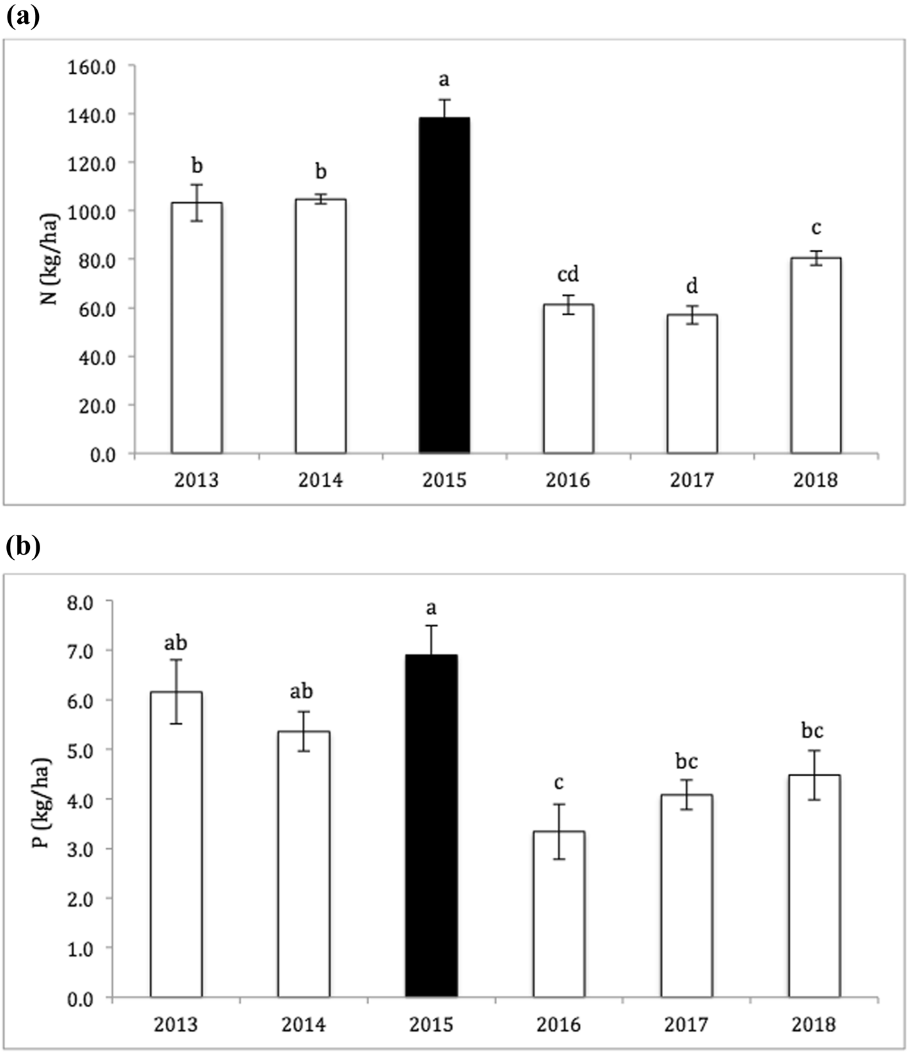

Figure 4. Total nitrogen **a** and phosphorus **b** fluxes (kg/ha) in the phenological years (July to June) previous to and after Hurricane Patricia in the tropical dry forest in Chamela, Jalisco, Mexico. Each bar represents the mean (± 1SE) of five long-term monitoring plots, one per watershed. The dark bar indicates the year of Hurricane Patricia landfall. ANOVAs for N and P fluxes were statistically significant at $p < 0.001$. Bars with no common letters are significantly different at $p < 0.05$ after a Tukey HSD test. Rainfall (June to the following May) was: 1,070 mm (2013), 1,506 mm (2014), 904.5 mm (2015), 641.5 mm (2016), 732 mm (2017), and 1,027 mm (2018).

(Martínez-Yrízar and others 2018; this study) and the increased accumulation of coarse woody debris (O. Galáz personal communication) attributed to Patricia disturbance suggest that dissolved organic *N* and *P* losses from the watersheds may have been significant, as was the case after Jova, especially regarding *P* (Jaramillo and others 2018).

The early consequences of Patricia on litterfall nutrients were evident in two different contexts: a) in the increased litterfall *N* and *P* concentrations 2–3 months after hurricane landfall, with a peak in December 2015, and b) in the greatly reduced *N* and *P* fluxes following the hurricane (November–June). Here, we propose three potential mechanisms, not mutually exclusive, to account for the higher nutrient concentrations following the hurricane, all related to rainfall and wind consequences on ecosystem structure and functioning. First, the enhanced soil moisture conditions from high rainfall during and up to two months after the hurricane (Maass and others 2018) may have promoted late-season soil nutrient release and uptake in undamaged plant species. Our studies have previously shown that soil *N* and *P* availability in the Chamela TDF increase in response to water inputs from rainfall (Campo and others 1998;

Montaño and others 2007) and from leaching of soluble nutrient forms from litter on the forest floor (Anaya and others 2007). Also, root-nodule death due to plant damage of *N*-fixing legume species, highly abundant in this forest (Durán and others 2002; Lott 2002; González-Ruiz and others 2008), and its subsequent mineralization, may have further increased soil *N* availability, while reducing *P* demand. Second, the drastic changes in canopy structure and cover (Parker and others 2018) and the high number of tall and hard-wood trees felled by the hurricane wind-force (Jiménez-Rodríguez and others 2018; Paz and others 2018) could have resulted in other undamaged lower-statured trees or shrubs and vines making a large contribution of high-nutrient post-hurricane litterfall. Third, as suggested by Killingbeck (1988), hurricane-affected plants without mechanical injury may have experienced lower nutrient resorption efficiencies, thus producing higher nutrient litter. This increase in litterfall nutrient concentrations is similar to what was documented after Hurricane Jova for *P*, although not for *N* (Jaramillo and others 2018). Experimental results from Puerto Rico have also shown short-term increases in both *N* and *P* concentrations in litterfall after simulated hurricane canopy disturbance (Silver and others 2014). Such response, however, was not evident after typhoon disturbance in a subtropical forest of Taiwan (Lin and others 2003), highlighting that the effects and responses are complex and may vary greatly among forests exposed to tropical storms, as suggested by Heartsill-Scalley and López-Marrero (2021). The high input of nutrient-enriched litter and debris to the forest floor, in these cases due to hurricane disturbance, may have short- and longer-term ecosystem consequences. For example, nutrient-rich litter decomposes faster than non-enriched litter (Enriquez and others 1993; Ostertag and others 2003; Xu and others 2004b) leading to increased soil nutrient availability and faster nutrient cycling rates. Also, *C* and nutrient storage in both surface- and subsoils may increase up to a decade after hurricane disturbance due to debris deposition (Gutiérrez del Arroyo and Silver 2018).

The other early consequence of Patricia was the greatly reduced *N* and *P* fluxes, especially in the months following the hurricane, which were due to tree mortality, branch fall, and reduced productivity (Martínez-Yrízar and others 2018). Such reductions in seasonal and annual *N* and *P* fluxes were evident up to 44 months after Patricia. This response differs from other studies that have shown these fluxes to increase up to six months after hurricane landfall in Hawai'i (Herbert and others 1999) and to the relatively rapid recovery of biogeochemical processes in the Chamela TDF itself after Jova (Jaramillo and others 2018). Thus, the observed short-term reduction in productivity resulting from Patricia in the Chamela TDF (Martínez-Yrízar and others 2018) is evident in the nutrient fluxes still in the short term. For example, the mean annual *N* and *P* fluxes in the three post-Patricia years (2016–2018) represent only 57% (*N*) and 64% (*P*) of pre-Patricia annual fluxes and are also smaller than those in any other non-hurricane years (Jaramillo and others 2018; Jaramillo unpublished). These results add to the argument that TDF resistance to hurricanes in Chamela is low (Jaramillo and others 2018; Martínez-Yrízar and others 2018) and suggest that forest recovery after Patricia will take longer than after Jova, supporting our hypothesis. Our findings highlight the importance of considering not only the consequences of high-intensity storms on forest resistance and recovery, but also the legacy effects from previous hurricane disturbances, especially in forests infrequently subjected to hurricane landfall.

The Chamela TDF has been exposed in recent decades not only to these two hurricanes from the Pacific coast (Category 2 Jova in 2011 and Category 4 Patricia in 2015), but also to a hurricane originated in the Atlantic basin plunging inland over Central and Western Mexico (category 2 Dean 2007; Table 2). The consequences of each event greatly differed. Arrival of Hurricane Dean to the

Table 2. Litterfall Nitrogen and Phosphorus Fluxes (kg/ha) After Three Hurricanes in the Tropical Dry Forest in Chamela, Jalisco, Mexico

Hurricane	Rainfall (mm)	Nitrogen (kg/ha)	Phosphorus (kg/ha)	Reference
Dean (2007)	942.5	93.7	5.1	Jaramillo unpublished
Jova (2011)	1,178.5	101.6	7.9	Jaramillo and others (2018)
Patricia (2015)	904.5	138.1	6.9	This study

Nutrient fluxes comprise the phenological years (July to June). Rainfall (mm) corresponds to the hydrological year (June–May) in each case. Hurricane Dean was category 2 upon its second landfall in the Gulf of Mexico, which brought the unusual rainfall to Chamela. Hurricanes Jova and Patricia were category 2 and 4, respectively, at landfall in the Chamela region.

Chamela TDF produced the highest monthly rainfall in our long-term data set with 561 mm delivered in August of that year, resulting also in the highest sediment yield off the watersheds on record (Maass and others 2018). Despite the high-intensity rainfall and the overall wet year of 2007 (18% above the mean), Hurricane Dean did not significantly modify the annual litterfall *N* and *P* fluxes, which were close to the mean *N* (93.4 kg/ha) and *P* (5.8 kg/ha) fluxes in non-hurricane years (for example, 2010 and 2012, calculated from Jaramillo and others 2018) and even lower than in other very humid, non-hurricane years such as 2013 and 2014 (with 1,070 mm and 1,506 mm, respectively, this study) and 1999 with 1,131 mm (98.6 kgN/ha; 5.5 kgP/ha; Jaramillo unpubl.). In contrast, hurricanes Jova and Patricia affected the TDF ecosystem structure and functioning in a variety of ways (see Álvarez-Yépiz and others 2018, *Special Issue*). Landfall of these hurricanes, with the concurrent strong wind-force and heavy rainfall, resulted in higher litterfall *N* and *P* fluxes than during Dean. However, comparing between Jova and Patricia, the annual *N* flux was higher after the latter, but the annual *P* flux was lower, suggesting differing forest *N* and *P* responses to repeated hurricane disturbance. We hypothesize that lower litterfall *P* concentrations (nearly half the values) and annual *P* flux after Patricia than after Jova possibly reflect a short-term consequence of high dissolved organic P losses in runoff after Jova, which represented 148% of the *P* flux from vegetation to the soil (Jaramillo and others 2018). Also, we suggest that the annual *P* flux attributed to Jova (~ 8 kgP/ha), the highest in our long-term data (Jaramillo unpublished), may represent a threshold to the *P* cycle in the Chamela TDF. On the other hand, litterfall *N* cycling after Patricia does represent the largest annual *N* flux in our more than 25 y record (Jaramillo unpublished).

Finally, our results indicate that the extreme hydrometeorological event of Hurricane Patricia overrode the *N* cycling resistance documented after Hurricane Jova in the Chamela TDF (Jaramillo and others 2018). Also, recovery of litterfall *N* and *P* cycling to pre-disturbance levels has not occurred three years after Patricia, suggesting that forest resilience (sensu Hodgson and others 2015) has been reduced, at least in the short term, when compared to the forest response after Jova. Surely, the process of recovery will continue, although different aspects of ecosystem structure (for example, height or canopy cover) and functioning (for example, nutrient cycling or primary productivity) will do so at different time scales (Parker and others 2018). This may be particularly relevant to forest dynamics and recovery due to the evidence of tropical cyclone activity migrating towards the coasts (Wang and Toumi 2021) and to current projections indicating a higher proportion of categories 4 and 5 tropical cyclones, and thus higher and more destructive wind speeds, with global warming (Seneviratne and others 2021).

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