



# Resilience of soil nutrient availability and organic matter decomposition to hurricane impact in a tropical dry forest ecosystem<sup>☆</sup>

Mayra E. Gavito<sup>a,\*</sup>, Ana Lidia Sandoval-Pérez<sup>a</sup>, Karem del Castillo<sup>a</sup>, Daniel Cohen-Salgado<sup>a</sup>,  
María Elena Colarte-Avilés<sup>a</sup>, Francisco Mora<sup>a</sup>, Angélica Santibáñez-Rentería<sup>a</sup>, Ilyas Siddique<sup>a,b</sup>,  
Claudia Urquijo-Ramos<sup>a</sup>

<sup>a</sup> Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México-campus Morelia, Antigua Carretera a Pátzcuaro 8701 Colonia Exhacienda San José de la Huerta, CP 58190 Morelia, Michoacán, Mexico

<sup>b</sup> Centro de Ciências Agrárias, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil<sup>†</sup>

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## ABSTRACT

Hurricanes Jova and Patricia were the first hurricanes in recent history to make landfall on the tropical dry forest ecosystem of the Pacific coast of Mexico. We examined the resilience of soil N and P availability and organic matter decomposition to the effects of both hurricanes in pastures, successional fields and old-growth forests of this region. We evaluated resistance by comparing measurements made before and after each hurricane. We also examined temporal trends to test if variables non-resistant to Jova recovered during the four-year period between both hurricanes. We considered resilient those variables that either showed resistance or were not resistant but showed recovery. We hypothesized that decomposition and soil nutrient availability would increase shortly due to the massive incorporation of high-quality decomposing materials after both hurricanes, especially under land covers with more woody vegetation, and return to pre-hurricane values within a couple of years. Our tests showed that most variables measured were not resistant to either hurricane and that the direction or magnitude of change sometimes differed between hurricanes. There was a fourfold increase in soil available N after hurricane Jova and a twofold increase after hurricane Patricia. Soil available P changed little over the entire period. Total litter stocks resisted hurricane passage and differed only among land covers whereas litter C, N and P stocks changed with the hurricane and became more similar in all land covers over the following three years. The soil N peak caused a decrease in the C:N and N:P ratios in the litter produced from the leaf flush some months after Hurricane Jova. This decrease was measured, however, only two years after hurricane Jova in total accumulated litter. Decomposition rates of local recent litter decreased after hurricane Jova and increased after hurricane Patricia but recovered within two years after hurricane Jova. Decomposition of a standard material in all sites, used as a control, showed a decreasing trend suggesting a continuous reduction in decomposer activity after hurricane Jova. Overall there were smaller differences among land covers than we had expected and their inter-annual fluctuations in most variables were surprisingly similar. We conclude that nutrient availability and decomposition were in general not resistant but returned to pre-hurricane levels within the four years between hurricane Jova and hurricane Patricia. Therefore, these ecosystem functions seemed resilient, at least to hurricane Jova.

## 1. Introduction

Hurricane main impacts on soils derive from the extraordinary inputs of organic material and alterations of the local environment as a result of the stripping of leaves and branches (Shiels and González, 2014). Litterfall pulses are often reported in regions impacted by

hurricanes (Lugo, 2008). They contain detached green leaves with more nutrients than the senesced leaves that usually fall, but also more twigs with low nutrient content. Therefore, the combination of both materials in hurricane inputs may result in decomposing materials that are nutrient-rich (Lodge and McDowell, 1991; Lodge et al., 1991), or of average quality (Herbert et al., 1999).

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\* Corresponding author.

E-mail address: [mgevito@cieco.unam.mx](mailto:mgevito@cieco.unam.mx) (M.E. Gavito).

<sup>†</sup> Present address.

Climatic conditions, litter chemistry and decomposer activity are recognized worldwide as the main drivers of organic matter decomposition (García-Palacios et al., 2016) and hurricanes may temporarily alter all of them. Following a large litterfall pulse, decomposition is the next process that may be disturbed in soil as a consequence of the hurricane passage. Decomposition in tropical regions is mainly driven by water availability but at local scales site-specific factors may complicate predictions (Powers et al., 2009). Consequently, the final incorporation of nutrients from hurricane inputs to the soil depends on the effects of the existing local conditions (e.g. soil types, topography, vegetation, history of management) and the temporary changes induced by the hurricane (e.g. microclimate) on the decomposition process (Shiels and González, 2014). The litterfall pulses undergoing decomposition trigger nutrient mineralization and immobilization processes that may induce only ephemeral changes in nutrient pools (Silver et al., 1996) or cause long-lasting alterations in relation to pre-hurricane conditions (Scatena et al., 1996).

In regions undergoing constant hurricane pressure, hurricanes are considered agents of ecosystem structuring and post-hurricane reorganization patterns are well documented and understood (Lugo, 2008). In the Chamela-Cuixmala Biosphere Reserve region on the Pacific coast of Mexico, however, hurricanes Jova (2011, category 2) and Patricia (2015, category 4) were the two first hurricanes in recent history that made landfall, advancing several kilometers inland and causing extensive damage, mainly by wind disturbance (Brennan, 2012; Kimberlain et al., 2016). Hurricanes are frequent in this region (Blake et al., 2009) but they usually lose strength immediately after landfall. Hurricanes Jova and Patricia represent therefore extraordinary events in this tropical dry forest region. Soil functional responses to two close events causing unusual litterfall pulses and the resilience of key soil functions may not be straightforward predictable from those observed in regions where hurricane damage is frequent. Resilience is the capacity of a system to maintain its function when exposed to disturbance and has two measurable components, resistance (capacity to withstand disturbance without changing), and recovery (capacity to return to pre-disturbance conditions when the system did not resist) (Hodgson et al., 2015). Both components together represent resilience. Most studies on hurricane effects on vegetation or soil have focused on the immediate and short-term changes originated by the hurricane, that means on resistance, but few have explicitly examined recovery.

On the coast of Jalisco, marked seasonality of rainfall and low soil nutrient availability drive foliar nutrient resorption and later shedding of nutrient-poor senescing leaves during the dry season, especially for phosphorus (Jaramillo et al., 2011; Rentería and Jaramillo, 2011; Rentería et al., 2005). These materials accumulate on the floor until the rainy season starts providing water for decomposition, a process showing a strong relationship with large (> 10 mm) rainfall events (Anaya et al., 2012). Decomposing materials rapidly release nutrients during the first weeks of the rainy season and produce a pulse of available nutrients (Montaño et al., 2009). The pulse can be of different magnitudes depending on the nutrient form and on the land cover type since managed areas, covered predominantly by extensive pastures, have smaller litter stocks resulting from lower tree cover, grazing and burning practices (Ayala-Orozco et al., 2017) and consequently smaller nutrient pulses and overall lower fertility than successional and old-growth forests (Sandoval-Pérez et al., 2009).

The effects of two extraordinary disturbances altering the normal inputs of organic materials and resource conservation mechanisms are worth investigating, especially in the context of global change. Most ecological studies examining hurricane impacts have been conducted in old-growth forests. However, tropical landscapes are composed of a mixture of land-uses and land-covers differing in microclimatic conditions, and on the effects of previous human activities, like reductions in ecosystem nutrient pools and soil fertility (Ayala-Orozco et al., 2017; Cao and Sánchez-Azofeifa, 2017; García-Oliva and Jaramillo, 2011; Lebrija-Trejos et al., 2011; Pineda et al., 2013). Previous human

perturbations may interact with subsequent hurricane disturbance, modifying the effects of the latter relative to old-growth forests (McGroddy et al., 2004). Analyzing the responses of other common land covers is therefore essential to support regional modeling exercises and landscape projections of hurricane disturbances. The intense land-use and land-cover change dynamics of tropical dry forest regions in the Americas (Portillo-Quintero and Sánchez-Azofeifa, 2010) and current climate alterations make it especially relevant to study whether extraordinary hurricane disturbances affect ecosystem processes such as nutrient availability and organic matter decomposition temporarily or cause long-lasting alterations.

Given the intrinsic rainfall variability of this ecosystem (Maass and Burgos, 2011), more than an unusual rainfall input, the most remarkable change induced in the soil by hurricanes Jova and Patricia was the unusual timing, quantity and type of plant material entering the necromass (Jaramillo et al. under review for this issue). Therefore, this study aimed at (1) documenting the changes in quality of decomposing materials, decomposition rates and soil N and P availability after hurricanes Jova and Patricia in sites with different land covers in the Chamela region, and (2) evaluating the resilience of the land cover types to hurricane disturbance by testing the resistance and examining the recovery patterns, as suggested by Hodgson et al. (2015), of litter quality, litter decomposition and nutrient availability. We hypothesized that, as a result of massive green-leaf incorporation in most sites, especially those with more woody vegetation, litter quality, litter decomposition and nutrient availability would increase temporarily and then return to pre-hurricane values after a couple of years.

## 2. Materials and methods

### 2.1. Study region

The study sites are located on the Pacific coast in the State of Jalisco, Mexico, (19°29'N, 105°01'W, Table A1). This tropical dry forest (TDF) area has a mean annual temperature of 25 °C and rainfall concentrated between June and October (García-Oliva et al., 1991), with an annual mean of 795 mm. The study area includes the Chamela-Cuixmala Biosphere Reserve and approximately a 30-km zone around the reserve with small villages and areas transformed to agricultural or pasture use. Poorly developed soils, Regosols, Lixisols, Cambisols, and Phaeozems (FAO/WRB), formed over tuffs and granite predominate in the region (Cotler et al., 2002).

### 2.2. Land covers

This region was colonized by people mostly after 1970 (Castillo et al., 2005). Land conversion and secondary succession have produced a landscape mosaic covered mainly by dry forest (75%, including the reserve) and deforested areas (16%) (Sánchez-Azofeifa et al., 2009), with pastures and successional fields on the hills and agriculture on the plains (Burgos and Maass, 2004). The study was conducted in a set of 21 study sites including active pastures, successional fields and old-growth forests representative of the low-hill landscape. Pastures under extensive cattle ranching are covered by the introduced forage grasses *Panicum maximum* Jacq. (Guinea grass) and *Cenchrus ciliaris* L. (buffel grass) as well as forbs, thorny shrubs and tree resprouts that are controlled mainly with trimming and regular burning (Burgos and Maass, 2004; Trilleras et al., 2015).

Pastures are frequently left without maintenance (seeding, trimming, burning) allowing succession and the rapid recovery of a closed canopy with substantial woody species richness and basal area within the first 10–15 years (Maza-Villalobos et al., 2011; Mora et al., 2015). The old-growth forest is a highly diverse tropical dry forest (Lott, 1993), dominated by deciduous trees 4–15 m in height. Common tree species include *Bursera* spp., *Jatropha simpatala*, *Caesalpinia eriostachys*, *Caesalpinia coriaria*, *Cordia alliodora*, and *Lonchocarpus constrictus*.

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