Tropical storms and ecological research in the Luquillo Experimental Forest: A bibliography

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Data collection for long-term research at the Luquillo Experimental Forest in the aftermath of Hurricanes Irma and María. (Photo: Tamara Heartsill Scalley)

Introduction

Tropical storms cause a range of short-, medium-, and long-term effects on forest ecosystems; they influence forest structure, dynamics, composition, and diversity of biota, as well as the abiotic component that supports ecosystem processes and functions. Storms also affect the provision of ecosystem services that are vital to sustain life and necessary to support ecosystem functions. The passage of atmospheric systems also provides opportunities to conduct studies allowing knowledge production, thus broadening understanding of these disturbances on forest ecosystems.

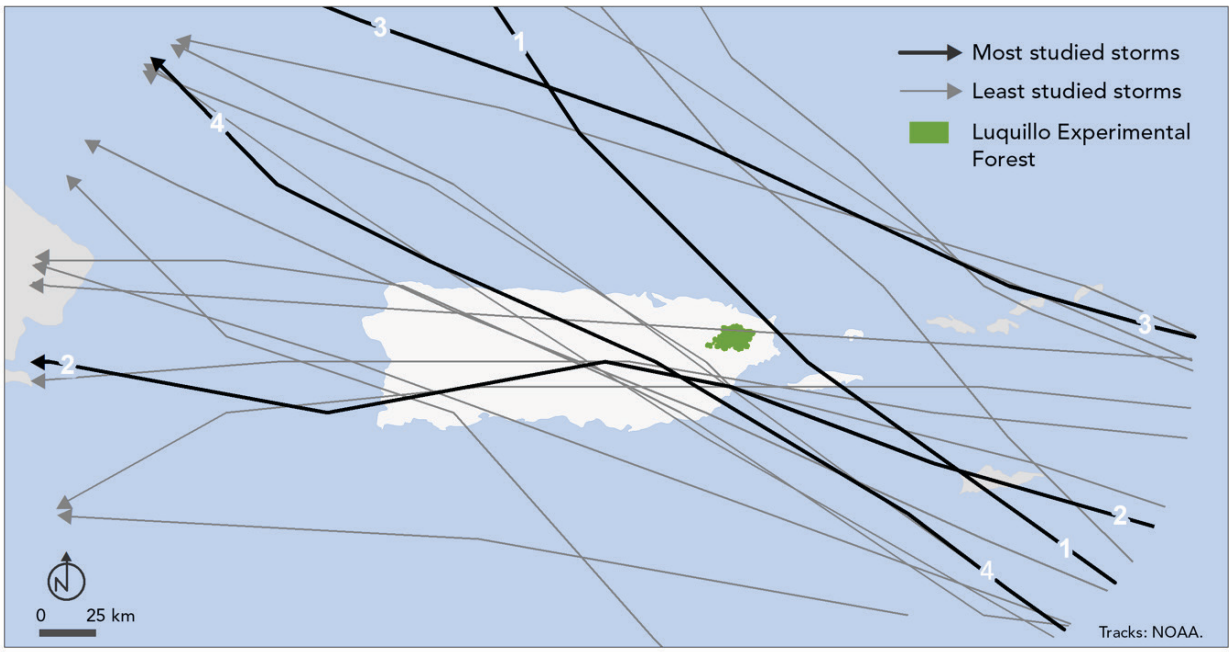
Tropical storms over and near the Luquillo Experimental Forest (also known as El Yunque National Forest, hereinafter LEF) and their effects on forest ecosystems have been an important research focus. This is particularly true for the last three decades, after the passage of Hurricane Hugo in 1989 (see section **Studies of tropical storms and forests in the Luquillo Experimental Forest: An overview**). In this publication, we provide a bibliography of 203 peer-reviewed articles identified through a systematic literature review regarding ecological research conducted in the LEF on storms and forests (see section **About the development of the bibliography**). Through this bibliography, the reader will be acquainted with the research conducted in the LEF. While we are aware the bibliographic list does not contain all published storm and forest studies in the LEF, it does provide a broad resource for researchers, managers, and practitioners to support current and future research and management practices. Next, we provide an overview of the research conducted based on the 203 articles that constitute this bibliography.

Studies of tropical storms and forests in the Luquillo Experimental Forest: An overview

Studies of tropical storms and forest ecosystems have produced a wealth of knowledge in the LEF, particularly during the last three decades. An assessment of the 203 articles identified 22 hurricanes and tropical storms, 12 of which made landfall, as the focus of the research, and subsequently, the focus of analysis of the articles (**Map 1**). Assessment and observation of storm effects in the LEF began with a category-3 hurricane that made landfall in 1932, locally known as Hurricane San Ciprián. This was followed by studies on Tropical Storm Baker (1950) and Hurricane Betsy (1956, locally known as Hurricane Santa Clara). After these disturbances, other storms affected the LEF and have been the subject of research. However, Hurricanes Hugo, Georges, Irma, and María generated the most research on the effects of hurricane disturbance on ecosystem processes in the LEF. Hurricane Hugo was a category-4 hurricane, the center of which crossed the island of Vieques and northeastern Puerto Rico in 1989. It was

the first major hurricane to strike Puerto Rico since Hurricane San Ciprián in 1932, nearly 60 years earlier. Nine years after Hurricane Hugo, Hurricane Georges made landfall in 1998 as a category-3 hurricane, also affecting the LEF. In 2017, in the span of two weeks, Puerto Rico was impacted by two major hurricanes: category-5 Hurricane Irma to the northeast of the island and category-4 Hurricane María that made landfall in the southeast.

The effects of some hurricanes were studied individually; in other cases, the effects of two or more hurricanes were considered. Hurricanes Hugo, Georges, Irma, and María, specifically, permitted the study of long-term, comparative effects of intense hurricanes on the LEF ecosystems. Moreover, experimental research with simulated climatic conditions and hurricane effects has been conducted, for example, the Canopy Trimming Experiment and the Tropical Responses to Altered Climate Experiment.



Map 1. Trajectories of storms studied in the examined articles. The most studies storms, identified by number, were: 1. Hugo (1989), 2. Georges (1998), 3. Irma (2017), and 4. María (2017). Four other studied storms passed outside of the area shown on this map and are not included.

A categorization of the 203 articles regarding tropical storm and forest studies in the LEF revealed that:

- Most articles (164 or 81%) addressed storm effects on the biotic component of forest ecosystems, while the remaining 19% focused on abiotic components.
- Plants were the focus of analysis of articles studying biotic-related ecosystem aspects (104 articles), followed by animals (58 articles), and bacteria and fungi (2 articles).
- Most plant-focused articles studied hurricane effects on woody vegetation, especially trees (83 articles), while a smaller portion studied lianas (woody climbers) and pines.
- Storm effects on non-woody vegetation were also studied, mostly on palms (21 articles) and herbaceous plants, ferns, vines, orchids, and hemi-epiphytes.
- Storm effects on insects were the focus of analysis in animal-related articles (21 articles), followed by birds and snails (10 articles each). Although in smaller numbers, amphibian, mammal, spider, shrimp, and reptile studies were included in the animal-related articles.
- Less than a quarter of articles (39 or 19%) studied storm effects on forest ecosystem abiotic components. These mostly focused on fluxes and accumulation of nutrients (29 articles) but were also associated with decomposition, photosynthesis, and microclimate changes.

About the development of the bibliography

Articles provided in this bibliography were identified through a systematic literature review of storms and ecological research conducted in the LEF between 1900 and 2023, following the procedure of López-Marrero and others (2019). The search was conducted using the Web of Science Citation Index. Search terms included a combination of keywords, including the geographical area ("Puerto Rico") and associated terms regarding the hazard of interest (hurricane*, storm*, cyclone*) and the ecosystem of interest (forest*). We also included regional journals (i.e., Caribbean Naturalist, Caribbean Geography, Caribbean Journal of Science, and Caribbean Studies) in the review process since they are often not in databases such as Web of Science. Moreover, we assessed the bibliographic sections of published literature review articles, summary articles, and introductions or conclusions of special issues about storms and forests in Puerto Rico to identify relevant articles that may not have been identified through Web of Science and regional journal search.

This bibliography includes the 203 article citations and abstracts (when available) as presented in the original article. References are listed alphabetically (based on the first author's last name). When the article is open source, a hyperlink is provided for downloading the article.

Reference

López Marrero, T.; Heartsill Scalley, T.; Rivera López, C.F. [and others]. 2019. Broadening Our Understanding of Hurricanes and Forests in the Caribbean Island of Puerto Rico: Where and What Should We Study Now? Forests 10: 710. https://doi.org/10.3390/f10090710

Acknowledgements

We would like to acknowledge Carlos F. Rivera López for his assistance in conducting the bibliographic search. We thank the personnel from the International Institute of Tropical Forestry – National Forest Service Library for searching and providing articles included in the bibliography and uploading articles in Treesearch. Tamara Enz is acknowledged for editing this fact sheet, and Cynthia Lee Gotay Colón is acknowledged for the publication layout (following Raghu Consbruck's original designs for the El Yunque project). This publication is part of a research and science delivery project funded through the USDA Forest Service.

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How to cite this publication

López Marrero, T.; Heartsill Scalley, T. 2024. Tropical storms and ecological research in the Luquillo Experimental Forest: A bibliography. USDA Forest Service, Region 8. 136 p.

For more information

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BIBLIOGRAPHY

Acevedo, M.A.; Clark, D.; Fankhauser, C. [and other]. 2022. No evidence of predicted phenotypic changes after hurricane disturbance in a shade-specialist Caribbean anole. Biology Letters. 18: 20220152. https://doi.org/10.1098/rsbl.2022.0152
Download: https://royalsocietypublishing.org/doi/epdf/10.1098/rsbl.2022.0152

Extreme climatic events (ECEs) such as hurricanes have been hypothesized to be a major driving force of natural selection. Recent studies argue that, following strong hurricane disturbance, Anolis lizards in the Caribbean undergo selection for traits such as longer forelimbs or smaller body sizes that improve their clinging ability to their substrates increasing their chances of surviving hurricane wind gusts. Some authors challenge the generalization of this hypothesis arguing that other mechanisms may explain these phenotypic changes or that they may not necessarily be generalizable across systems. To address this issue, we compared body size and relative forelimb length of *Anolis gundlachi*, a trunk-ground anole living in closed-canopy forests in Puerto Rico, before, four months after, and 15 months after Hurricanes Irma and Maria in 2017. Overall, our results show no clear evidence of a temporal decrease in body size or increase forelimb length (relative to body size) challenging the generalizability of the clinging ability hypothesis. Understanding how animals adapt to ECE is an emerging field. Still, we are quickly learning that this process is complex and nuanced.

Ackerman, J.D.; Moya, S. 1996. Hurricane Aftermath: Resiliency of an Orchid-Pollinator interaction in Puerto Rico. Caribbean Journal of Science. 32(4): 369-374.
Download: https://www.fs.usda.gov/research/treesearch/66358

The impact of severe habitat disturbance on plants and animals is often dramatically negative, but across species and guilds there is considerable variance. The effects of hurricane damage exemplify this phenomenon. When most organisms are adversely affected, it is expected that the dynamics of their interactions will also be altered. The consequences of a direct hit by Hurricane Hugo, a category 4 storm, on a plant-pollinator interaction was investigated by comparing pre-hurricane (1981–1985) with post-hurricane data (1989-1990). The nectarless, self-compatible *Epidendrum ciliare* L. (Orchidaceae) is pollinated by *Pseudosphinx tetrio* (L.) (Sphingidae), a large hawkmoth. Despite severe habitat alteration and some plant damage (uprooting, breakage and sun scorching), flowering phenology was apparently unaltered. Pollinator service was different from that of previous years in that mom flowers were visited (57% vs. 28-41%). The higher number of effective visits increased pollinarium removals, but the number of pollinia depositions remained about the same (11% vs. 11–15%). Fruit fates differed among seasons. Post-hurricane loss of fruits to rat predation was higher than previous years, but the proportion of fruits reaching maturity was similar to prehurricane seasons. Final fruit set after the hurricane (5.3%) fell within the range of previous years.

Although details of the plant-pollinator dynamics were altered, the short-term consequences of hurricane induced damages were apparently minimal.

Alonso-Rodríguez, A.M.; Wood, T.E.; Torres-Díaz, J. [and others]. 2022. Understory plant communities show resistance to drought, hurricanes, and experimental warming in a wet tropical forest. Frontiers in Forests and Global Change. 5: 733967.
https://doi.org/10.3389/ffgc.2022.733967
Download: https://www.frontiersin.org/articles/10.3389/ffgc.2022.733967/full

Global climate change has led to rising temperatures and to more frequent and intense climatic events, such as storms and droughts. Changes in climate and disturbance regimes can have non-additive effects on plant communities and result in complicated legacies we have yet to understand. This is especially true for tropical forests, which play a significant role in regulating global climate. We used understory vegetation data from the Tropical Responses to Altered Climate Experiment (TRACE) in Puerto Rico to evaluate how plant communities responded to climate warming and disturbance. The TRACE understory vegetation was exposed to a severe drought (2015), 2 years of experimental warming (4 C above ambient in half of the plots, 2016–2017 and 2018–2019), and two major hurricanes (Irma and María, September 2017). Woody seedlings and saplings were censused yearly from 2015 to 2019, with an additional census in 2015 after the drought ended. We evaluated disturbance-driven changes in species richness, diversity, and composition across ontogeny. We then used Bayesian predictive trait modeling to assess how species responded to disturbance and how this might influence the functional structure of the plant community. Our results show decreased seedling richness after hurricane disturbance, as well as increased sapling richness and diversity after warming. We found a shift in species composition through time for both seedlings and saplings, yet the individual effects of each disturbance were not significant. At both ontogenetic stages, we observed about twice as many species responding to experimental warming as those responding to drought and hurricanes. Predicted changes in functional structure point to disturbance driven functional shifts toward a mixture of fast-growing and drought tolerant species. Our findings demonstrate that the tropical forest understory community is more resistant to climatic stressors than expected, especially at the sapling stage. However, early signs of changes in species composition suggest that, in a warming climate with frequent droughts and hurricanes, plant communities might shift over time toward fast-growing or drought tolerant species.

Angulo-Sandoval, P.; Fernández-Marín, H.; Zimmerman, J.K. [and other]. 2004. Changes in Patterns of Understory Leaf Phenology and Herbivory following Hurricane Damage. Biotropica. 36(1): 60-67. https://doi.org/10.1111/j.1744-7429.2004.tb00296.x
Download: https://www.fs.usda.gov/treesearch/pubs/30192

Hurricanes are important disturbance events in many forested ecosystems. They can have strong effects on both forest structure and animal populations, and yet few studies have considered the impacts on plant–animal interactions. Reduction of canopy cover by severe winds increases light availability to understory plants, providing an opportunity for increased growth. An increase in light availability should cause an increase in annual production of leaves and a more even production throughout the year (i.e., less seasonality in production). This change will affect the availability of food resources to folivorous insects that feed primarily on young leaves; outbreaks of these insects could nullify the temporary advantage of increased understory light levels. On 21 September 1998, Hurricane Georges struck Puerto Rico, providing an excellent opportunity to determine the effect of the hurricane on leaf production and herbivory in the forest understory by comparing post-hurricane data with data obtained from a previous study conducted at the same site. Eight species were analyzed at El Verde Field Station, a wet forest site in eastern Puerto Rico. For the eight species combined, there was an increase in number of leaves produced after the hurricane and a more even seasonal pattern of leaf production, as predicted. Levels of herbivory were much lower (2.03%) after the hurricane compared with pre hurricane conditions (16.05%), indicating that increased light availability to understory plants was not offset by increased herbivory. Lower levels of herbivory were possibly due to herbivore satiation, changes in leaf chemistry, changes in herbivore populations, changes in herbivore predator populations, or a combination of two or more of these factors.

Barberena-Arias, M.F.; Aide, T.M. 2002. Variation in Species and Trophic Composition of Insect Communities in Puerto Rico. Biotropica. 34(3): 357-367.
https://doi.org/10.1111/j.1744-7429.2002.tb00549.x

Insects are important participants in many ecosystem processes, but the effects of anthropogenic and natural disturbances on insect communities have been poorly studied. To describe how disturbances affect insect communities, we addressed two questions: Do insect communities return to a pre-hurricane composition? And how do insect communities change during succession? To answer these questions, we studied insect communities in a chronosequence of two abandoned pastures (5 yr and 32 yr) and a mature forest (>80 yr) that were recently disturbed by two hurricanes (Hurricane Hugo, 1989; Hurricane Georges, 1998). Although insect abundance and richness fluctuated during the study, all sites returned to pre-hurricane (Hurricane Georges) abundance and richness in less than one year. All trophic categories present before Hurricane Georges were present after the hurricane, but richness within categories fluctuated greatly. Insect richness did not increase during succession; the 5 yr site had the highest richness, the >80 yr site had an intermediate richness, and the 32 yr site the lowest. Nevertheless, the species composition of the two forested sites was different

in comparison to the 5 yr site. These results suggest that trophic structure varies little in time and space, but the species composition within each trophic category is highly variable.

Basnet, K. 1993. Recovery of a tropical rain forest after hurricane damage. Vegetatio. 109: 1-4. https://doi.org/10.1007/BF00149540

More than a year after Hurricane Hugo damaged a Puerto Rican tropical rain forest, recovery of the forest was assessed by observing resprouting of damaged trees in eleven transects which were established before the hurricane in 1989. In each transect, I relocated and identified standing trees and observed if they were resprouting after injury. I found that resprouting was rapid and depended on species. There was no significant relationship between sprouting and diameter classes of trees. This study suggests that resprouting of damaged trees plays major roles in the recovery of the tropical forests which are prone to hurricanes and are in non-equilibrium state.

Basnet, K.; Likens, G.E.; Scatena, F.N. [and other]. 1992. Hurricane Hugo: Damage to a Tropical Rain Forest in Puerto Rico. Journal of Tropical Ecology. 8: 47-55. https://doi.org/10.1017/S0266467400006076

Hurricane Hugo of September 1989 caused severe damage to the rain forest in the north-east corner of Puerto Rico. We assessed the severity of damage distributed in space, species, and size-classes of trees in the Bisley Watersheds of the Luquillo Experimental Forest. We analyzed pre- and post-hurricane data for vegetation from transects established in 1987 and 1988. The severity of damage was significantly greater in valleys than on ridges and slopes. All the species except *Dacryodes excelsa*, *Sloanea berteriana*, and *Guarea Guidonia* showed 100% severe damage. Large trees (> 70 cm DBH) were highly susceptible to hurricane damage, but there was no clear pattern in the small size-classes. *D. excelsa* (tabonuco) was the most resistant to damage by the hurricane. Tabonuco which has extensive root-grafts and root anchorage to bedrock and subsurficial rocks, apparently can survive frequent hurricanes and continue as a dominant species in this montane tropical rain forest. The high frequency of hurricanes, which can override other ecological and topographic factors, may largely determine the overall spatial pattern of species in this rain forest.

Basnet, K.; Scatena, F.N.; Likens, G.E. [and other]. 1993. Ecological Consequences of Root Grafting in Tabonuco (*Dacryodes excelsa*) Trees in the Luquillo Experimental Forest, Puerto Rico. Biotropica. 25(1): 28-35. https://doi.org/10.2307/2388976
Download: https://www.fs.usda.gov/research/treesearch/66359

Root grafting was commonly found in tabonuco (*Dacryodes excelsa Vahl*), a dominant tree

species of tabonuco forest in the subtropical wet forest of Puerto Rico. Over 60 percent of all stems and basal area of tabonuco occurred in unions, clumps of trees interconnectedby root grafts. Self and intraspecific grafting were extensive, while interspecific graft in was not common in tabonuco trees. Seedlings and saplings did not show any grafting, probably because of their size or age. Grafted trees were taller and had a smaller crown/DBH ratio. Hurricane damage was significantly higher in isolated individual tabonuco trees than those in unions. Weak relationships between diameter, class, area, and size of union, and inter-tree distances and the sum of the trunk circumferences of the two nearest neighbors suggested that a noncompetitive force such as root grafting was more important than competitive forces in maintaining the unions of tabonuco, and thus the forest community. A conceptual model of the costs and gains of tabonuco in unions is presented.

Beard, K.H.; Vogt, K.A.; Vogt, D.J. [and others]. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecological Monographs. 75(3): 345-361. https://doi.org/10.1890/04-1114
Download: https://www.fs.usda.gov/research/treesearch/66360

Little is known about ecosystem-level responses to multiple, climatic disturbance events. In the subtropical forests of Puerto Rico, the major natural disturbances are hurricanes and droughts. We tested the ecosystem-level effects of these disturbances in sites with different land use histories. From 1989 to 1992, data were collected to determine the effects of Hurricane Hugo and two droughts on litterfall inputs, fine-root biomass, and decomposition rates in three topographic locations (stream, riparian, upslope) within two watersheds. From 1994 to 1998, we added a third watershed and an experiment in which coarse-wood levels were manipulated to simulate hurricane inputs. Data were collected on tree and palm growth rates, litterfall inputs, fine-root biomass, and decomposition rates. From 1994 to 1998, four hurricanes and three droughts were recorded. Measured parameters had unique responses and recovery rates to hurricanes and droughts. Litterfall inputs returned to long-term mean rates within one month following droughts and small-to-moderate hurricanes but required five years to recover after an intense hurricane. In contrast, fine-root biomass recovered seven months after an intense hurricane but failed to recover after five years following a severe drought. Despite the dramatic effects of these weather events on some ecosystem parameters, we found that aboveground measures of tree and palm growth were more affected by preexisting site conditions (e.g., nitrogen availability due to past land use activities) than hurricanes or droughts. The addition of coarse woody debris increased tree and palm growth, fine-root biomass, and litter production; however, in the case of tree and palm growth, this effect was least measurable in the sites with the highest productivity. We found that decomposition rates were more controlled by litter quality than weather conditions. In conclusion, we found that certain ecosystem structures (e.g., canopy structure and fine-root

biomass) generally recovered more slowly from disturbance events than certain ecosystem processes (e.g., plant growth rates, decomposition rates). We also found that past land use activities and disturbance legacies were important in determining the responses and recovery rates of the ecosystem to disturbance.

Beissinger, S.R.; Wunderle, J.M.; Meyers, J.M. [and others]. 2008. Anatomy of a bottleneck: Diagnosing factors limiting population growth in the Puerto Rican Parrot. Ecological Monographs. 78(2): 185-203. https://doi.org/10.1890/07-0018.1
Download: https://www.fs.usda.gov/treesearch/pubs/39757

The relative importance of genetic, demographic, environmental, and catastrophic processes that maintain population bottlenecks has received little consideration. We evaluate the role of these factors in maintaining the Puerto Rican Parrot (*Amazona vittata*) in a prolonged bottleneck from 1973 through 2000 despite intensive conservation efforts. We first conduct a risk analysis, then examine evidence for the importance of specific processes maintaining the bottleneck using the multiple competing hypotheses approach, and finally integrate these results through a sensitivity analysis of a demographic model using life-stage simulation analysis (LSA) to determine the relative importance of genetic, demographic, environmental, and catastrophic processes on population growth. Annual population growth has been slow and variable (1.0 6 5.2 parrots per year, or an average k¼1.05 6 0.19) from 16 parrots (1973) to a high of 40–42 birds (1997–1998). A risk analysis based on population prediction intervals (PPI) indicates great risk and large uncertainty, with a range of 22–83 birds in the 90% PPI only five years into the future. Four primary factors (reduced hatching success due to inbreeding, failure of adults to nest, nest failure due to nongenetic causes, and reduced survival of adults and juveniles) were responsible for maintaining the bottleneck. Egg hatchability rates were low (70.6% per egg and 76.8% per pair), and hatchability increased after mate changes, suggesting inbreeding effects. Only an average of 34% of the population nested annually, which was well below the percentage of adults that should have reached an age of first breeding (41–56%). This chronic failure to nest appears to have been caused primarily by environmental and/or behavioral factors, and not by nest-site scarcity or a skewed sex ratio. Nest failure rates from nongenetic causes (i.e., predation, parasitism, and wet cavities) were low (29%) due to active management (protecting nests and fostering captive young into wild nests), diminishing the importance of nest failure as a limiting factor. Annual survival has been periodically reduced by catastrophes (hurricanes), which have greatly constrained population growth, but survival rates were high under non-catastrophic conditions. Although the importance of factors maintaining the Puerto Rican Parrot bottleneck varied throughout the 30-year period of study, we determined their long-term influence using LSA simulations to correlate variation in demographic rates with variation in

population growth (k). The bottleneck appears to have been maintained primarily by periodic catastrophes (hurricanes) that reduced adult survival, and secondarily by environmental and/or behavioral factors that resulted in a failure of many adults to nest. The influence of inbreeding through reduced hatching success played a much less significant role, even when additional effects of inbreeding on the production and mortality of young were incorporated into the LSA. Management actions needed to speed recovery include (1) continued nest guarding to minimize the effects of nest failure due to nongenetic causes; (2) creating a second population at another location on the island—a process that was recently initiated—to reduce the chance that hurricane strikes will cause extinction; and (3) determining the causes of the low percentage of breeders in the population and ameliorating them, which would have a large impact on population growth.

Bloch, C.P.; Willig, M.R. 2006. Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. Journal of Tropical Ecology. 22: 111-122. https://doi.org/10.1017/S0266467405002853
Download: https://www.fs.usda.gov/treesearch/pubs/30051

Large-scale natural disturbances, such as hurricanes, can have profound effects on animal populations. Nonetheless, generalizations about the effects of disturbance are elusive, and few studies consider long-term responses of a single population or community to multiple large-scale disturbance events. In the last 20 y, two major hurricanes (Hugo and Georges) have struck the island of Puerto Rico. Long-term population trends of 17 species of terrestrial gastropod were evaluated to determine whether gastropods respond to hurricane disturbances in a consistent fashion. Some species increased, some decreased, and some exhibited no simple trend in density or spatial variability following disturbance. In addition, some species responded differently to the two hurricanes with respect to population density, absolute spatial variability, or relative spatial variability. Population responses probably hinge on trade-offs between sensitivity tomicroclimatic changes and resource availability resulting from the relocation of biomass from the canopy to the forest floor. The historical context within which a hurricane occurs may be as important, or more so, than the intensity of the storm, per se.

Bloch, C.P.; Higgins, C.L.; Willig, M.R. 2007. Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness. Oikos. 116: 395-406. https://doi.org/10.1111/j.0030-1299.2007.15391.x

Distributions of species often exhibit nested structure, such that assemblages at species-poor sites are proper subsets of taxa at more species-rich sites. Traditionally, this has been viewed as a large-scale biogeographic pattern and treated implicitly as static from a temporal perspective. Nonetheless, recent work suggests that nestedness may arise at multiple spatio-

temporal scales. A 13-year data set encompassing the effects of two largescale natural disturbances (hurricanes Hugo and Georges) on terrestrial gastropod assemblages was used to test the hypothesis that changes in species composition resulting from disturbance alter the degree of nestedness exhibited over time at two spatial scales. Gastropod assemblages were least nested immediately following disturbance, and nestedness increased thereafter. Although land-use history influenced the degree of nestedness, trajectories of nestedness following disturbance were similar irrespective of disturbance history or hurricane identity. The effects of hurricanes with respect to nestedness of terrestrial gastropods may be general and predictable, even though species respond to hurricanes in disparate fashions. By damaging some localities within the forest more severely than others, a hurricane dismantles extant patterns of species composition and severs connections among sites, as inhospitable microclimatic conditions limit dispersal of gastropods. As time passes and the forest canopy regenerates, conditions ameliorate, and movement among sites becomes more frequent. Thus, a conclusion based on a single time period may not characterize the study system in general. Consequently, explanations for nested structure that incorporate variability in ecological as well as evolutionary time will improve the applicability and comparability of nested subsets analysis across study systems.

Boose, E.R.; Foster, D.R.; Fluet, M. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs. 64(4): 369-400.
https://doi.org/10.2307/2937142

Hurricanes represent an important natural disturbance process to tropical and temperate forests in many coastal areas of the world. The complex patterns of damage created in forests by hurricane winds result from the interaction of meteorological, physiographic, and biotic factors on a range of spatial scales. To improve our understanding of these factors and of the role of catastrophic hurricane wind as a disturbance process, we take an integrative approach. A simple meteorological model (HURRECON) utilizes meteorological data to reconstruct wind conditions at specific sites and regional gradients in wind speed and direction during a hurricane. A simple topographic exposure model (EXPOS) utilizes wind direction predicted by HURRECON and a digital elevation map to estimate landscape-level exposure to the strongest winds. Actual damage to forest stands is assessed through analysis of remotely sensed, historical, and field data. These techniques were used to evaluate the characteristics and impacts of two important hurricanes: Hurricane Hugo (1989) in Puerto Rico and the 1938 New England Hurricane, storms of comparable magnitude in regions that differ greatly in climate, vegetation, physiography, and disturbance regimes. In both cases patterns of damage on a regional scale were found to agree with the predicted distribution of peak wind gust velocities. On a landscape there was also good agreement between patterns of forest damage

and predicted exposure in the Luquillo Experimental Forest in Puerto Rico and the town of Petersham, Massachusetts. At the Harvard and Pisgah Forests in central New England the average orientation of wind-thrown trees was very close to the predicted peak wind direction, while at Luquillo there was also good agreement, with some apparent modification of wind direction by the mountainous terrain. At Harvard Forest there was evidence that trees more susceptible to windthrow were felled earlier in the storm. This approach may be used to study the effects of topography on wind direction and the relation of forest damage to wind speed and duration; to establish broad-scale gradients of hurricane frequency, intensity, and wind direction for particular regions; and to determine landscape-level exposure to long-term hurricane disturbance at particular sites.

Brokaw, N.V.L.; Grear, J.S. 1991. Forest Structure Before and After Hurricane Hugo at Three Elevations in the Luquillo Mountains, Puerto Rico. Biotropica. 23(4a): 386-392. https://doi.org/10.2307/2388256

Hurricane Hugo struck Puerto Rico on 18 September 1989 and radically altered the canopy structure of forests in the Luquillo Mountains. We measured canopy structure before and after the hurricane in hectare-sized plots of "tabonuco forest" (subtropical wet forest) at 350 m elevation, "colorado forest" (lower montane wet forest) at 750 m, and "cloud forest" (lower montane rain forest) at 1000 m. In all three plots the chief effect of the hurricane was to reduce significantly the vegetation cover in upper height intervals. Foliage profiles (showing percent vegetation cover in height intervals above ground) changed significantly, average maximum canopy height decreased (by as much as 50%), and the amount of low canopy area (vegetation <=2m high) markedly increased (up to 60-fold) in all three plots. In the colorado forest plot the hurricane caused more damage on ridges than in valleys; whereas, the cloud forest plot sustained equal damage on windward and leeward slopes. Overall, the hurricane altered forest structure so much that forest composition and dynamics could be affected for many years. Local variation in hurricane damage can contribute to forest complexity in the Luquillo Mountains.

Burrowes, P.A.; Hernández-Figueroa, A.D.; Acevedo, G.D. [and others]. 2021. Can artificial retreat sites help frogs recover after severe habitat devastation? Insights on the use of "coqui houses" after Hurricane Maria in Puerto Rico. Amphibian & Reptile Conservation. 15(1): 57-70.
Download: https://amphibian-reptile-conservation.org/pdfs/Volume/Vol_15_no_1/ARC_15_1_%5BGeneral_Section%5D_57-70_e274.pdf

On September 2017, Hurricane Maria swept over Puerto Rico as a Category 4 storm. Severe canopy loss, augmentation of forest floor debris, and a significant increase in temperature and

light reaching the understory were among the most evident changes at El Yunque National Forest, where a population of *Eleutherodactylus coqui* frogs has been monitored over the past 30 years. When sampling was re-established, the frogs could be heard calling, but it was very difficult to find them among the complexity of vegetation in the forest floor. We inferred that canopy disturbance had left frogs without optimal arboreal habitats for retreat, nocturnal perching, feeding, and reproductive activities, and wondered whether they would use artificial habitats placed in the forest understory. To test this, two types of artificial habitats (i.e., "coqui houses") were introduced in the forest understory, consisting of either open PVC pipes or single-entrance natural bamboo shoots. Surveys were conducted twice a month for 15 months in an experimental transect with coqui houses, and a control transect without them. Data were collected on the occupancy rate of the artificial sites, type of usage, time of day occupied, and the number of *E. coqui* observed. The effects of time since the hurricane, microhabitat temperature, type of coqui house, and seasonality on the occupancy rate were also evaluated. Results showed that coquis used bamboo houses mostly during daytime as retreat and nesting sites, whereas the PVC houses were used mostly at night as calling sites. Daytime occupancy of coqui houses showed a significant bell-shaped pattern over time since the hurricane. This may be explained by a steady increase in usage after severe forest damage, a peak during the stressful cool-dry season, and a decline afterwards as the forest began to recover. No differences were found in frog counts between experimental and control transects, probably because the coquiscould also hide among the fallen vegetation, but either disparities in forest conditions or inappropriateness of the methods for estimating population numbers may have overshadowed this effect. Coquis used artificial houses more often during the most stressful environmental conditions, suggesting that these shelters may serve to enhance habitat quality for amphibians after extreme weather events.

Calderón-Acevedo, C.A.; Rodríguez-Durán, A; Soto-Centeno, J.A. 2021. Effect of land use, habitat suitability, and hurricanes on the population connectivity of an endemic insular bat. Scientific Reports. 11: 9115. https://doi.org/10.1038/s41598-021-88616-7
Download: https://www.nature.com/articles/s41598-021-88616-7

Urbanization and natural disasters can disrupt landscape connectivity, effectively isolating populations and increasing the risk of local extirpation particularly in island systems. To understand how fragmentation affects corridors among forested areas, we used circuit theory to model the landscape connectivity of the endemic bat *Stenoderma rufum* within Puerto Rico. Our models combined species occurrences, land use, habitat suitability, and vegetation cover data that were used either as resistance (land use) or conductance layers (habitat suitability and vegetation cover). Urbanization affected connectivity overall from east to west and underscored protected and rustic areas for the maintenance of forest corridors. Suitable

habitat provided a reliable measure of connectivity among potential movement corridors that connected more isolated areas. We found that intense hurricanes that disrupt forest integrity can affect connectivity of suitable habitat. Some of the largest protected areas in the east of Puerto Rico are at an increasing risk of becoming disconnected from more continuous forest patches. Given the increasing rate of urbanization, this pattern could also apply to other vertebrates. Our findings show the importance of maintaining forest integrity, emphasizing the considerable conservation value of rustic areas for the preservation of local biodiversity.

Campos-Cerqueira M, Aide TM. 2021. Impacts of a drought and hurricane on tropical bird and frog distributions. Ecosphere. 12(1): e03352. https://doi.org/10.1002/ecs2.3352
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3352

During the last few decades, much attention has focused on how global change is affecting the environment and species distributions. Land-use change is still the major cause of species declines worldwide, but changes in species distributions have been documented even in pristine and protected areas. Here, we document the distribution dynamics of 26 species of frogs and birds within a Caribbean protected area between 2015 and 2019. Specifically, we document species occupancy and detectability in 59 sites along three elevational transects within the El Yunque National Forest in Puerto Rico. Species were sampled using acoustic recorders, species identification algorithms, and post-classification validation. The study period included a severe drought (2015–2016) and a category 4 hurricane (2017). The distribution of most frog species did not change significantly during the study period. In contrast, the distributions of the bird species contracted between the 2015 and 2016 pre-hurricane surveys. This contraction coincides with a severe drought that peaked after the 2015 survey. The response of bird species after H. Maria was heterogeneous. Our results suggest that for many species, particularly birds, the 2015–2016 drought in Puerto Rico had a greater negative effect than H. Maria. The difference in the response of the bird and frog communities is likely related to their abundance at the site level, their ability to disperse, and temporal patterns of reproduction. If a site is occupied by a frog species, it could easily include 100s of individuals, and even if condition worsens, over a relatively short period the species will continue to occupy the site. In contrast, a site may only be occupied by one or a few individuals of birds. Birds have also higher dispersal abilities than frogs. Furthermore, Puerto Rican frogs reproduce year-round, whereas birds concentrate their reproduction during a few months in the wet season. Future climate scenarios predict a decrease in total precipitation and an increase in droughts for the region, which emphasizes the need to consider the diversity of changes that will be associated with future climate change.

Canham, C.D.; Thompson, J.; Zimmerman, J.K. [and other]. 2010. Variation in Susceptibility to Hurricane Damage as a Function of Storm Intensity in Puerto Rican Tree Species. Biotropica. 42(1): 87-94. https://doi.org/10.1111/j.1744-7429.2009.00545.x

One of the most significant challenges in developing a predictive understanding of the long-term effects of hurricanes on tropical forests is the development of quantitative models of the relationships between variation in storm intensity and the resulting severity of tree damage and mortality. There have been many comparative studies of interspecific variation in resistance of trees to wind damage based on aggregate responses to individual storms. We use a new approach, based on ordinal logistic regression, to fit quantitative models of the susceptibility of a tree species to different levels of damage across an explicit range of hurricane intensity. Our approach simultaneously estimates both the local intensity of the storm within a plot and the susceptibility to storm damage of different tree species within plots. Using the spatial variation of storm intensity embedded in two hurricanes (Hugo in 1989 and Georges in 1998) that struck the 16 ha Luquillo Forest Dynamics Plot in eastern Puerto Rico, we show that variation in susceptibility to storm damage is an important aspect of life history differentiation. Pioneers such as *Cecropia schreberiana* are highly susceptible to stem damage, while the late successional species *Dacryodes excelsa* suffered very little stem damage but significant crown damage. There was a surprisingly weak relationship between tree diameter and the susceptibility to damage for most of the 12 species examined. This may be due to the effects of repeated storms and trade winds on the architecture of trees and forest stands in this Puerto Rican subtropical wet forest.

Cantrell, S.A.; Molina, M. Lodge, D.J. [and others]. 2014. Effects of a simulated hurricane disturbance on forest floor microbial communities. Forest Ecology and Management. 332: 22-31. https://doi.org/10.1016/j.foreco.2014.07.010
Download: https://www.fs.usda.gov/treesearch/pubs/47198

Forest floor microbial communities play a critical role in the processes of decomposition and nutrient cycling. The impact of cultivation, contamination, fire, and land management on soil microbial communities have been studied but there are few studies of microbial responses to the effects of tropical storms. The Canopy Trimming Experiment was executed in the Luquillo Experimental Forest of Puerto Rico to decouple two prominent effects of a hurricane—canopy opening and debris deposition on the forest floor—on forest biota and processes. We studied the independent and interactive hurricane effects of canopy openness and debris deposition on the relative abundance and diversity of microorganisms in soil and leaf litter using ester link fatty acids methyl esters (EL-FAME) analysis, and terminal restriction fragment length polymorphism (TRFLP) profile. Non-metric multi-dimensional scaling analysis of soil FAME showed soil microbial community composition was significantly different between pre- and

post-hurricane periods including in the unmanipulated plots and among blocks, but there was no significant separation among treatments. This shows that there are strong spatiotemporal dynamics in the structure of soil microbial communities which masked hurricane effects (canopy opening and deposition of green debris). The degree of difference among treatments decreased with time in soil which suggests that our study may have started too late after the manipulations and therefore missed the effects of canopy opening and debris addition. This reflects the resilience of the soil microbial communities. The richness of soil bacterial TRF's however, showed a significant positive response to added debris. Neither fungal nor bacterial NMDS clusters for leaf microbial communities showed significant grouping by treatment, time or litter cohorts. Significant differences were observed through time for fungal diversity in green leaves and for both bacterial and fungal diversity in senesced leaves. Senesced leaves microbial succession apparently stopped when both the canopy and debris were removed, and there was a suggestive trimming by time interaction which reflects the susceptibility of the leaf litter microbial community. Our findings contribute to the understanding of how microbial community structures can be affected by hurricane disturbances and forestry management practices that remove canopy and debris from the forest floor, and shows the need to analyze the microbial community immediately after the disturbance. Short-term changes in microbial communities due to forest disturbances can have significant implications for litter decomposition, soil organic matter accumulation, nutrient cycling, and food web dynamics in tropical forests. All of these factors should be taken into consideration when selecting the appropriate forest management practice.

Chevalier, H.; Brokaw, N.V.L.; Ward, S.E. [and others]. 2022. Aboveground carbon responses to experimental and natural hurricane impacts in a subtropical wet forest in Puerto Rico. Ecosphere. 13(4): e4041. https://doi.org/10.1002/ecs2.4041
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.4041

Climate change and disturbance make it difficult to project long-term patterns of carbon sequestration in tropical forests, but large ecosystem experiments in these forests can inform predictions. The Canopy Trimming Experiment (CTE)manipulates two key components of hurricane disturbance, canopy openness and detritus deposition, in a tropical forest in Puerto Rico. We documented how the CTE and a real hurricane affected tree recruitment, biomass, and aboveground carbon storage over 15 years. In the CTE treatments, we trimmed branches, but we did not fell trees. We expected that during the 14-year period after initial canopy trimming, regrowth of branches and stems and stem recruitment stimulated by increased light and trimmed debris would help restore biomass and carbon loss due to trimming. Compared to control plots, in the trimmed plots recruitment of palms and dicot trees increased markedly after trimming, and stem diameters of standing trees increased.

Data showed that recruitment of small trees adds little to aboveground carbon, compared to the amount in large trees. Nevertheless, this response restored pretreatment biomass and carbon in the experimental period. In particular, the experimental additions of trimmed debris on the forest floor seemed to stimulate increase in above ground carbon. Toward the end of the experimental period, Hurricane Maria (Category 4 hurricane) trimmed and felled some trees but reduced aboveground carbon less in the plots (including untrimmed plots) than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming could also restore aboveground carbon in the forest after a severe hurricane in the same time span. However, Hurricane Maria, unlike the trimming treatments, felled large trees, and it may be that with predicted, more frequent severe hurricanes, that the continued loss of large trees would over the long term decrease aboveground carbon stored in this Puerto Rican forest and likewise in other tropical forests affected by cyclonic storms.

Chinea, J.D. 1999. Changes in the herbaceous and vine communities at the Bisley Experimental Watersheds, Puerto Rico, following Hurricane Hugo. Canadian Journal of Forest Research. 29: 1433-1437. https://doi.org/10.1139/x99-108
Download: https://www.fs.usda.gov/treesearch/pubs/30307

While herbaceous species and vines constitute a minor portion of the biomass in tropical closed forest ecosystems, they account for a substantial portion of the diversity of these ecosystems and become more conspicuous after natural disturbances. This study describes the changes in abundance and diversity of the herbs and vines during 5 years following Hurricane Hugo at the Bisley Experimental Watersheds, Puerto Rico. The cover of herbs, ferns, and vine species was sampled within a 5-m2 area in 25 randomly chosen circular permanent plots within the 13 ha of these watersheds. Sampling was done 12, 18, 36, 48, and 60 months after the hurricane. One year after the hurricane the overall mean herbaceous cover in the watersheds was 55%. Four years later, the cover and species richness of herbs and vines, but not ferns, had been significantly reduced. The only change in species diversity (*H'*) was a significant increase in ferns. These changes are explained in terms of the extent and spatial variability of the hurricane damage, as well as changes in the tree component of this ecosystem.

Clark, K.E.; Stallard, R.F.; Murphy, S.F. [and others]. 2022. Extreme rainstorms drive exceptional organic carbon export from forested humid-tropical rivers in Puerto Rico. Nature Communications. 13: 2058. https://doi.org/10.1038/s41467-022-29618-5
Download: https://www.nature.com/articles/s41467-022-29618-5

Extreme rainfall in Puerto Rico leads to some of the highest particulate organic carbon yields. Here the authors find that global estimates of carbon export may be underestimated

by up to 9% because of a lack of studies in the tropics. Extreme rainfall events in the humid-tropical Luquillo Mountains, Puerto Rico export the bulk of suspended sediment and particulate organic carbon. Using 25 years of river carbon and suspended sediment data, which targeted hurricanes and other large rainstorms, we estimated biogenic particulate organic carbon yields of 65 +/- 16 tC km(-2) yr(-1) for the Icacos and 17.7 +/- 5.1 tC km(-2) yr(-1) for the Mameyes rivers. These granitic and volcaniclastic catchments function as substantial atmospheric carbon-dioxide sinks, largely through export of river biogenic particulate organic carbon during extreme rainstorms. Compared to other regions, these high biogenic particulate organic carbon yields are accompanied by lower suspended sediment yields. Accordingly, particulate organic carbon export from these catchments is under predicted by previous yield relationships, which are derived mainly from catchments with easily erodible sedimentary rocks. Therefore, rivers that drain petrogenic-carbon-poor bedrock require separate accounting to estimate their contributions to the geological carbon cycle.

Comita, L.S.; Uriarte, M.; Forero-Montaña, J. [and others]. 2018. Changes in Phylogenetic Community Structure of the Seedling Layer Following Hurricane Disturbance in a Human-Impacted Tropical Forest. Forests. 9: 556. https://doi.org/10.3390/f9090556
Download: https://www.mdpi.com/1999-4907/9/9/556

Disturbance plays a key role in shaping forest composition and diversity. We used a community phylogeny and long-term forest dynamics data to investigate biotic and abiotic factors shaping tropical forest regeneration following both human and natural disturbance. Specifically, we examined shifts in seedling phylogenetic and functional (i.e., seed mass) community structure over a decade following a major hurricane in a human-impacted forest in Puerto Rico. Phylogenetic relatedness of the seedling community decreased in the first five years post-hurricane and then increased, largely driven by changes in the abundance of a common palm species. Functional structure (based on seed mass) became increasingly clustered through time, due to canopy closure causing small-seeded, light-demanding species to decline in abundance. Seedling neighbor density and phylogenetic relatedness negatively affected seedling survival, which likely acted to reduce phylogenetic relatedness within seedling plots. Across the study site, areas impacted in the past by high-intensity land use had lower or similar phylogenetic relatedness of seedling communities than low-intensity past land use areas, reflecting interactive effects of human and natural disturbance. Our study demonstrates how phylogenetic and functional information offer insights into the role of biotic and abiotic factors structuring forest recovery following disturbance.

Comita, L.S.; Thompson, J.; Uriarte, M. [and others]. 2010. Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. Ecological Applications. 20(5): 1270-1284. https://doi.org/10.1890/09-1350.1

Human-impacted forests are increasing in extent due to widespread regrowth of secondary forests on abandoned lands. The degree and speed of recovery from human disturbance in these forests will determine their value in terms of biodiversity conservation and ecosystem function. In areas subject to periodic, severe natural disturbances, such as hurricanes, it has been hypothesized that human and natural disturbance may interact to either erase or preserve land use legacies. To increase understanding of how interactions between human and natural disturbance influence forest regeneration and recovery, we monitored seedlings in a human- and hurricane-impacted forest in northeastern Puerto Rico over a ~10-yr period and compared seedling composition and dynamics in areas that had experienced high- and low-intensity human disturbance during the first half of the 20th century. We found that land use history significantly affected the composition and diversity of the seedling layer and altered patterns of canopy openness and seedling dynamics following hurricane disturbance. The area that had been subject to high-intensity land use supported a higher density, but lower diversity, of species. In both land use history categories, the seedling layer was dominated by the same two species, *Prestoea acuminata* var. *montana* and *Guarea guidonia*. However, seedlings of secondary-successional species tended to be more abundant in the high-intensity land use area, while late-successional species were more abundant in the low-intensity area, consistent with patterns of adult tree distributions. Seedlings of secondary-forest species showed greater increases in growth and survival following hurricane disturbance compared to late-successional species, providing support for the hypothesis that hurricanes help preserve the signature of land use history. However, the increased performance of secondary-forest species occurred predominantly in the low-intensity land use area, suggesting that hurricanes act to homogenize differences in species composition between areas with differing land use histories by increasing secondary-forest species regeneration in areas that experienced little direct human disturbance. Our results suggest that, through effects on seedling dynamics, hurricanes may extend the signature of land use history beyond the average recovery time of forests not subject to intense natural disturbance events.

Comita, L.S.; Uriarte, M.; Thompson, J. [and others]. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. Journal of Ecology. 97: 1346-1359. https://doi.org/10.1111/j.1365-2745.2009.01551.x
Download: https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2745.2009.01551.x

(1) Many forests experience periodic, large-scale disturbances, such as hurricanes and cyclones, which open the forest canopy, causing dramatic changes in understorey light conditions and seedling densities. Thus, in hurricane-impacted forests, large variations in

abiotic and biotic conditions likely shape seedling dynamics, which in turn will contribute to patterns of forest recovery. (2) We monitored 13, 836 seedlings of 82 tree and shrub species over 10 years following Hurricane Georges in 1998 in a subtropical, montane forest in Puerto Rico. We quantified changes in the biotic and abiotic environment of the understorey and linked seedling dynamics to changes in canopy openness and seedling density, and to spatial variation in soil type, topography and tree density. (3) Canopy openness was highest when first measured after Hurricane Georges and dropped significantly within c. 3years, while seedling densities remained high for c. 5 years post-hurricane. When all species and census intervals were analysed together, generalized linear mixed effects models revealed that canopy openness, seedling and adult tree densities were significant drivers of seedling survival. (4) The relative importance of abiotic and biotic factors changed over time. Separate analyses for each census interval revealed that canopy openness was a significant predictor of survival only for the first census interval, with lower survival at the highest levels of canopy openness. The effect of conspecific seedling density was significant in all intervals except the first, and soil type only in the final census interval. (5) When grouping species into life-history guilds based on adult tree susceptibility to hurricane damage, we found clear differences among guilds in the effects of biotic and abiotic factors on seedling survival. Seedlings of hurricane-susceptible and intermediate guilds were more strongly influenced by canopy openness, while seedlings of the hurricane-resistant group were less affected by conspecific seedling density. Individual species-level analyses for 12 common species, however, showed considerable variation among species within guilds. (6) *Synthesis*. Our results suggest that hurricanes shape species composition by altering understorey conditions that differentially influence the success of seedlings. Thus, predicted increases in the intensity and frequency of hurricanes in the Caribbean will likely alter seedling dynamics and ultimately the species composition in hurricane-impacted forests.

Covich, A.P.; Crowl, T.A.; Johnson, S.L. [and others]. 1991. Post-Hurricane Hugo Increases in Atyid Shrimp Abundances in a Puerto Rican Montane Stream. Biotropica. 23(4a): 448-454. https://doi.org/10.2307/2388265

We report the first data on changes in tropical stream biota resulting from a major hurricane. Beginning in January 1989, we trapped freshwater shrimp, *Atya lanipes*, along 1200 m of a montane stream in the Luquillo Experimental Forest, Puerto Rico. Prior to Hurricane Hugo, shrimp densities were greater in the headwaters than at mid- and low elevation. In October 1989, one month after the hurricane, shrimp densities were reduced on average by 50 percent in the headwaters (apparently from washout) and increased by 80 percent at mid-elevation. From December 1989 to May 1990 overall shrimp densities increased rapidly to the highest abundances ever recorded. These densities most likely resulted from increased numbers

of shrimp that migrated upstream from riverine pools; and, from increased availability of unusually abundant food resources (decomposing leaves and algae) that increased recruitment of these generalized consumers. Benthic communities in forested, headwater streams are likely to be resilient after intermediate levels of disturbance, because rapid debris-dam formation increases retention of food resources and reduces washout of invertebrate consumers. However, storms generating greater stream flow and/or less wind than Hurricane Hugo could cause extensive, longer-lasting decreases of benthic-dwelling shrimp because of greater washout of both consumers and food supplies.

Covich, A.P.; Crowl, T.A.; Johnson, S.L. [and other]. 1996. Distribution and Abundance of Tropical Freshwater Shrimp Along a Stream Corridor: Response to Disturbance. Biotropica. 28(4a): 484-492. https://doi.org/10.2307/2389090

Different intensities and frequencies of disturbances can alter spatial and temporal patterns of abundances for coexisting species. We observed the effects of a high-flow event generated by Hurricane Hugo (19 September 1989) and below-normal stream flow during 1994 on freshwater shrimp populations in a tropical, montane stream. To determine if these different hydrologic regimes altered distributions of populations, we compared shrimp densities during three periods: pre-Hurricane Hugo (20 mo), post-Hurricane Hugo (50 mo), and low-flow (12 mo). There were significant differences in the relationships between locations of stream pools along an elevational gradient (300 to 470 m) and the abundances of two species of shrimp (*Atya lanipes* and *Xiphocaris elongata*) during these three periods. *Atypa* increased in density with increasing elevation in a consistent fashion during all three periods. Densities also increased during the post-Hugo and low-flow periods relative to the pre-Hugo baseline. *Xiphocaris* increased in density with increasing elevation during the pre- and post-Hugo periods, but density decreased with elevation during the low-flow period. Palaemonid species of predatory shrimp, *Macrobrachium carcinus* and *Macrobrachium crenulatum*, consistently decreased in density with elevation during all three periods of observation. Multiple regression analyses demonstrated high predictability of *Atya* density distributions based on volume, pool depth, and coefficient of variation of pool depth during the pre-Hugo baseline observations. Xiphocaris densities were positively associated with pool width and negatively associated with the coefficient of variation of pool width in the pre-Hugo period. However, physical variables did not predict *Atya* or *Xiphocaris* densities during the post-Hugo period. During the dry period, there was a negative association between *Atya* densities and pool depth and width, and a positive association with the coefficient of variation of pool depth. During the dry period, *Xiphocaris* densities were best predicted as a function of maximum depth; there was a negative association with the coefficient of variation of pool width. Pre-Hugo *Macrobrachium* densities were negatively associated with the coefficient of variation

of pool width, pool width-to-depth ratio, and elevation; in the post-Hugo and dry periods, *Macrobrachium* densities were best predicted by elevation. Mechanisms that likely cause these patterns of distribution include avoidance of predators coupled with active preference by prey species for pool habitats with low frequency of washout by storm flows, and with sufficient storage of food resources (microbially conditioned leaf detritus).

Covich, A.P.; Crowl, T.A.; Heartsill-Scalley, T. 2006. Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico. Journal of the North American Benthological Society. 25(1): 99-107. https://www.journals.uchicago.edu/doi/10.1899/0887-3593(2006)25[99:EODAHD]2.0.CO;2
Download: https://www.fs.usda.gov/treesearch/pubs/30048

Extreme events (hurricanes, floods, and droughts) can influence upstream migration of macroinvertebrates and wash out benthic communities, thereby locally altering food webs and species interactions. We sampled palaemonid river shrimp (*Macrobrachium* spp.), dominant consumers in headwaters of the Luquillo Mountains of northeastern Puerto Rico, to determine their distributions along an elevational gradient (274–456 m asl) during a series of disturbances (Hurricane Hugo in 1989, a drought in 1994, and Hurricane Georges in 1998) that occurred over a 15-y period (19882002).We measured shrimp abundance 3 to 6 times/y in Quebrada Prieta in the Espiritu Santo drainage as part of the Luquillo Long-Term Ecological Research Program. In general, *Macrobrachium* abundance declined with elevation during most years. The lowest mean abundance of Macrobrachium occurred during the 1994 drought, the driest year in 28 y of record in the Espiritu Santo drainage. *Macrobrachium* increased in abundance for 6 y following the 1994 drought. In contrast, hurricanes and storm flows had relatively little effect on *Macrobrachium* abundance.

Crow, T.R. 1980. A Rainforest Chronicle: A 30-Year Record of Change in Structure and Composition at El Verde, Puerto Rico. Biotropica. 12(1): 42-55. https://doi.org/10.2307/2387772

Measurements over approximately a 30-year period in a *Dacryodes-Sloanea* forest indicate two distinctive phases in stand development. Secondary species were common in the early stand (1940's), and rapid accumulations of biomass and basal area were measured. Many new species entered the stand, and the number of stems increased. In contrast, the stand of the 1970's approached steady-state for biomass and basal area accumulations, and, relative to earlier measurements, fewer stems and fewer species were recorded in the plot. This apparent dichotomy can be correlated to the periodic disturbance caused by tropical storms. The last severe hurricane to strike Puerto Rico occurred in 1932, 11 years prior to the establishment

of the El Verde plot. It is postulated that the early measurements reflect the rapid recovery of the stand following this hurricane, with both invading secondary species and residual primary species present in the stand. Subsequent perturbations (i.e., cutting and another storm) were insufficient to disrupt the unmistakable trend toward a mature forest and the stand quickly approached steady-state conditions.

Crowl, T.A.; McDowell, W.H.; Covich, A.P. [and other]. 2001. Freshwater shrimp effects on detrital processing and nutrients on a tropical headwater stream. Ecology. 82(3): 775-783. https://doi.org/10.2307/2680196

In this paper, we report on a whole-pool manipulation of leaf litter decomposition in a tropical stream following a hurricane. The study was designed to distinguish how decapod species comprising two functional feeding guilds alter rates and magnitudes of leaf litter processing and nutrient release linking the detrital food web with the overall producer-consumer food web. Streams of the Luquillo Experimental Forest, Puerto Rico, are dominated numerically by two freshwater shrimp species (*Atya lanipes* and *Xiphocaris elongata*). To determine how these shrimp affected detrital processing following large leaf inputs associated with a hurricane, we manipulated the presence or absence of two species of shrimp in six fenced pools of a headwater stream with hurricane levels of Cecropia leaf litter over a 23-d period. The experiment was designed to determine how the two different shrimp affected: (1) the rate and amount of size fractionation of leaf material; (2) the localized nutrient concentrations in the pools; and (3) the rate of particulate export from the pools. Both shrimp species influenced detrital processing, but in fundamentally different ways. *Xiphocaris* shred intact, large leaves and converted them into fine, medium, and coarse particulates. Through this conversion process *Xiphocaris* increased the concentration and rate of downstream transport of suspended particulate organic matter. *Xiphocaris* also significantly increased the concentration of both total dissolved nitrogen and dissolved organic carbon, likely by changing the surface area to volume ratio of organic particles. *Atya*, a scraper/filter feeder, caused a slight increase in rates of leaf breakdown as compared to controls at the end of the experiment but filtered out fine organic particulates, resulting in less downstream export. Both decapod species affected detrital processing, but in fundamentally different ways, illustrating the potential importance guild diversity may have in altering both particulate and nutrient availability to the rest of the food web. In addition, these results suggest that the presence of both feeding guilds can significantly influence ecosystem responses to severe, large-scale disturbance events.

Cruz-Mendoza, A.C.; Rivera-Milán, F.F.; Arendt, W.J. [and others]. 2023. Effects of Hurricanes Irma and Maria on Abundance and Occupancy of *Margarops fuscatus* (Pearly-eyed Thrasher) in the Luquillo Experimental Forest, Puerto Rico. Caribbean Naturalist. 92: 1-16.
Download: https://data.fs.usda.gov/research/pubs/iitf/ja_iitf_2023_arendt_001.pdf

Margarops fuscatus (Pearly-eyed Thrasher) is recognized for its vagility, dispersal ability, aggressive behavior, opportunistic diet, high reproductive potential, and ability to inhabit marginal habitats. Given these traits, we predicted that thrasher post-hurricane site occupancy and abundance in the first post-hurricane year (2018) after hurricanes Irma and María (2017) would change with elevation, forest type, and vegetation damage. To document the hurricanes' effects on thrasher site occupancy and abundance along an elevation gradient (150–1074 m a.s.l.) in the Luquillo Experimental Forest (LEF), we compared point-count results obtained before the hurricanes (1998, 2005) and after the hurricanes (2018). We estimated thrasher occupancy with a single-season model and abundance with an N-mixture single-season model, with year as a covariate in all models. Elevation (with a quadratic effect) was the most important covariate for site occupancy and abundance estimation. Occupancy across 110 count sites decreased from 0.77 (0.03 SE) in 1998 to 0.50 (0.03) in 2005 to 0.37 (0.03) in 2018 after the hurricanes. Abundance estimates decreased from an average of 11 (0.75 SE) individuals/site in 1998 to 4.39 (0.37) in 2005 and 2.33 (0.19) in 2018. Occupancy and abundance were highest at mid-elevation (400–800 m) sites in all years, and there was no evidence of a shift in elevational range after the 2 hurricanes in 2018. Despite post-hurricane occupancy and abundance declines, the Pearly-eyed Thrasher remains a potential threat as a predator and competitor of endangered wildlife in mid-elevation forests in the LEF.

Drew, A.P. 1998. Growth Rings, Phenology, Hurricane Disturbance and Climate in *Cyrilla racemiflora L.*, a Rain Forest tree of the Luquillo Mountains, Puerto Rico. Biotropica. 30(1): 35-49. https://doi.org/10.1111/j.1744-7429.1998.tb00367.x

The growth phenology of *Cyrilla racemiflora* L., the dominant tree species of the montane rain forest, (subtropical lower montane rain forest, sensu Holdridge) of the Luquillo Mountains of Puerto Rico was studied intensively during 1989, and then semiannually through mid-1993 to determine the periodicity of changes in xylem structure. Four trees at 770 m were monitored for flowering, branch elongation, leaf litterfall, and xylem cell growth and differentiation in the lower stem, and these events were related to local seasonal patterns of rainfall and temperature. Hurricane Hugo defoliated study trees in September, 1989. Bud-break and branch elongation in March, 1989 were followed by earlywood xylem cell production in the lower stem in April and the onset of flowering in May. Leaf litterfall was greatest between April and June, coinciding with peak branch growth and new leaf formation. Latewood xylem

was produced in December. The general phenological pattern was synchronized between trees and over study years. Vessel diameter and density were monitored along with thickness of earlywood and latewood and the former converted to vessel lumen area, a measure of xylem conductance capacity. Annual growth rings were formed with periods of earlywood and latewood production coinciding with traditional summer (rainy) and winter (dry) seasons, respectively, in the Luquillo Mountains. Hurricane defoliation was followed by heavy flowering in 1990, a year of reduced branch elongation and annual xylem ring width, and was associated with maximum vessel lumen area, as was flowering in 1989, prior to the hurricane. Hurricane Hugo provided a perturbation that, through its elicited stress response, allowed for the demonstration of the interplay between flowering, branching, structural growth of xylem, and xylem function.

Drew, A.P.; Boley, J.D.; Zhao, Y. [and others]. 2009. Sixty-two years of change in subtropical wet forest structure and composition at El Verde, Puerto Rico. Interciencia. 34(1): 34-40.
Download: https://www.fs.usda.gov/treesearch/pubs/35359

A plot established in 1943 in a subtropical wet forest at the Luquillo Experimental Forest of Puerto Rico has been assessed periodically for changes in species and size of all trees >4cm diameter. Forest dynamics on a 0.72ha plot (EV-3) at 400masl at El Verde show recovery principally from hurricanes of 1928 and 1932, timber stand improvement in 1958, and from Hurricanes Hugo and Georges in 1989 and 1998. Damage from Hurricane Hugo only temporarily slowed aboveground biomass accretion of the developing forest. Stand increases in basal area and biomass continue to be due principally to growth of the dominant overstory species, *Dacryodes excelsa* and *Manilkara bidentata*, ingrowth of which was stimulated by Hugo. The pioneer species *Cecropia schreberiana* filled gaps abundantly following the Hurricane and the understory tree *Psychotria berteriana* proliferated. Ingrowth of *Prestoea montana* has been greater than for all other species since 1976 and was stimulated by Hugo and Georges as well as prior hurricanes, so that by 2005 it was the most abundant species. Hurricane Hugo caused low mortality among the largest trees on the plot. As a few species have become more dominant species evenness has declined. Species richness is only slightly greater today than in 1943. Results are discussed in terms of "building" and "thinning" phases associated with major hurricanes. Hurricanes have stimulated the addition of species to the forest in "building years," but have maintained that richness in the intervening "thinning years", lending credence to the "intermediate disturbance hypothesis".

Encarnación-Ojeda, M.; Meléndez-Ackerman, E.; Hernández-Muñiz, R. 2021. Environmental correlates of leaf stress symptoms in the micro-orchid *Lepanthes woodburyana* following Hurricane María. Acta Científica. 32(1-3): 73-83. Download: https://www.fs.usda.gov/research/treesearch/66361

Cloud forest species face many threats including, but not limited to, climate change and increased extreme weather events. On September 20th, 2017, Hurricane Maria hit the island of Puerto Rico, changing the amount of coverage, structure, and microclimate of its forests. Cloud forest epiphytes can be particularly susceptible to such dramatic changes. Following Hurricane Maria, we studied the leaf characteristics potentially associated with reduced leaf health in the *Lepanthes woodburyana*, an epiphytic micro-orchid, endemic to Puerto Rico. We specifically assessed whether the environmental (e.g., microclimate, percent canopy cover, elevation) and biological factors intrinsic to the plant (e.g., plant size, life stage) were associated with variation in percent canopy cover, the number and the probability of occurrence of dark spots and discoloration on the leaves of L. woodburyana. We expected to find negative associations between variables related to plants that had dark spots and discoloration with forest cover and humidity, and positive associations between the occurrence of dark spots with plant size and temperature. Our results showed that dark spot formation was more frequent at lower elevations, open canopies and high temperatures, suggesting plant stress symptoms associated to canopy changes following hurricane events are not homogeneous throughout the forest.

Erickson, H.E.; Ayala, G. 2004. Hurricane-induced nitrous oxide fluxes from a wet tropical forest. Global Change Biology. 10: 1155-1162. https://doi.org/10.1111/j.1529-8817.2003.00795.x

Hurricane activity is predicted to increase over the mid-Atlantic as global temperatures rise. Nitrous oxide (N_2O), a greenhouse gas with a substantial source from tropical soils, may increase after hurricanes yet this effect has been insufficiently documented. On September 21, 1998, Hurricane Georges crossed Puerto Rico causing extensive defoliation. We used a before–after design to assess the effect of Georges on N_2O emissions, and factors likely influencing N_2O fluxes including soil inorganic nitrogen pools and soil water content in a humid tropical forest at El Verde, Puerto Rico. Emissions of N_2O up to 7 months post-Georges ranged from 5.92 to 4.26 ng cm−2 h−1 and averaged five times greater than fluxes previously measured at the site. N_2O emissions 27 months after the hurricane remained over two times greater than previously measured fluxes. Soil ammonium pools decreased after Georges and remained low. The first year after the hurricane, nitrate pools increased, but not significantly when compared against a single measurement made before the hurricane. Soil moisture and temperature did not differ significantly in the two sampling periods. These results suggest

that hurricanes increase N_2O fluxes in these forests by altering soil N transformations and the relative availabilities of inorganic nitrogen.

Everly, J.; Yee, D. 2023. Influence of a simulated hurricane on aquatic insect recolonization in the phytotelma of *Heliconia caribaea* (Heliciniacaea). Biotropica. 55(4): 1-11. https://doi.org/10.1111/btp.13235

Disturbances like hurricanes can affect diversity and community composition, which may in turn affect ecosystem function. We examined how a simulated hurricane disturbance affected insect communities inhabiting the phytotelma (plant-held waters) of Heliconia caribaea in the Luquillo Experimental Forest of eastern Puerto Rico, a tropical island that frequently experiences hurricanes. We hypothesized that disturbance would alter diversity and that larger Heliconia would attract more species following disturbance due to the area-diversity relationship described by the Theory of Island Biogeography. Individual flower parts (bracts) of Heliconia inflorescences (racemes) were artificially disturbed via removal of existing insect communities, then after refilling with water, cohorts of Heliconia were destructively sampled biweekly for 6 weeks to assess recolonization patterns of alpha (bract level), beta, and gamma (summed across bracts; raceme level) diversity over time and across raceme sizes. Although we found no support for our hypothesis about the effect of raceme size on recolonization, our hypothesis regarding recolonization patterns over time was supported; species richness, evenness, and abundance of bracts increased directly after the disturbance and then decreased below pre-disturbance levels, and community composition at the raceme level changed significantly over time during recolonization. β Diversity was also greater in smaller racemes compared to larger racemes, suggesting high heterogeneity across bracts of Heliconia racemes exacerbated by raceme size and age. Overall, our results highlight the importance of scale and appropriate measurements of diversity (particularly alpha) in experiments aiming to extrapolate conclusions about the ecological impacts of disturbances across different habitats and ecosystems.

Fernández, D.S.; Fetcher, N. 1991. Changes in Light Availability Following Hurricane Hugo in a Subtropical Montane Forest in Puerto Rico. Biotropica. 23(4a): 393-399. https://doi.org/10.2307/2388257

The changes in light availability in the understory of a subtropical wet forest (Luquillo Experimental Forest, Puerto Rico) were monitored after the passage of Hurricane Hugo on 18 September 1989 Gallium arsenide phosphide sensors were placed 1 m apart along a 32 m transect. Data were collected for periods of 7-10 d in October and December 1989, and in March, July, and November 1990. Daily histograms were generated for observations of

photosynthetic photon flux density (PPFD) taken every two seconds. Mean total daily PPFD was calculated for each sensor in each data set. During the 14 mo after the passage of the hurricane, the PPFD showed a highly skewed distribution with most values <200 mmol $m^{-2}s^{-1}$ The maximum spatial heterogeneity was observed in July 1990 because of the shading of some sensors by the growing pioneer vegetation. Median values of total daily PPFD for ten months after the hurricane ranged from 7.7 to 10.8 mol m-2s-1, which is similar to values previously observed for large (>400 m^2) treefall gaps. Median total daily PPFD fell to 0.8 mol m-2s-1 in November 1990 because of almost complete coverage of the transect by a canopy of *Cecropia schreberiana* Miq. *ex. C. peltata*. An analysis of semivariance was used to discern patterns of autocorrelation in total daily PPFD along the transect. Through March 1990 patches of high and low light separated by distances of 10-12 m were detected. By July 1990 the patchiness was replaced by a pattern that showed no autocorrelation at distances of 1 m or greater.

Flynn, D.F.B.; Uriarte, M.; Crk,T. [and others]. 2010. Hurricane Disturbance Alters Secondary Forest Recovery in Puerto Rico. Biotropica. 42(2): 149-157. https://doi.org/10.1111/j.1744-7429.2009.00581.x

Land-use history and large-scale disturbances interact to shape secondary forest structure and composition. How introduced species respond to disturbances such as hurricanes in post-agriculture forest recovery is of particular interest. To examine the effects of hurricane disturbance and previous land use on forest dynamics and composition, we revisited 37 secondary forest stands in former cattle pastures across Puerto Rico representing a range of exposure to the winds of Hurricane Georges in 1998. Stands ranged from 21 to > 80 yr since agricultural abandonment and were measured 9 yr posthurricane. Stem density decreased as stands aged, while basal area and species richness tended to increase. Hurricane disturbance exerted contrasting effects on stand structure, contingent on stand age. In older stands, the basal area of large trees fell, shifting to a stand structure characteristic of younger stands, while the basal area of large trees tended to rise in younger stands with increasing hurricane disturbance. These results demonstrate that large-scale natural disturbances can alter the successional trajectory of secondary forest stands recovering from human land use, but stand age, precipitation and soil series were better predictors of changes in stand structure across all study sites. Species composition changed substantially between census intervals, but neither age nor hurricane disturbance consistently predicted species composition change. However, exposure to hurricane winds tended to decrease the abundance of the introduced tree *Spathodea campanulata*, particularly in smaller size classes. In all sites the abundance of the introduced tree *Syzygium jambos* showed a declining trend, again most strongly in smaller size classes, suggesting natural thinning through succession.

Foster, D.R.; Fluet, M.; Boose, E.R. 1999. Human or Natural Disturbance: Landscape-Scale Dynamics of the Tropical Forests of Puerto Rico. Ecological Applications. 9(2): 555-572. https://doi.org/10.2307/2641144

Increasingly, ecologists are recognizing that human disturbance has played an important role in tropical forest history and that many assumptions concerning the relative importance of natural processes warrant re-examination. To assess the historical role of broad-scale human vs. natural disturbance on an intensively studied tropical forest we undertook a landscape-level analysis of forest dynamics in the Luquillo Experimental Forest (LEF; 10,871 ha) in eastern Puerto Rico. Using aerial photographs (1936 and 1989), GIS, a model of topographic exposure to hurricane winds, and historical data, we sought to: (1) document historical changes in extent, cover, and type of forest vegetation; (2) evaluate the distribution of land use and hurricane impacts; (3) assess the contributions of these processes in controlling current vegetation patterns; and (4) relate these results to ongoing ecological, conservation, and natural resource discussions. With > 1000 m of relief in the LEF, the broad vegetation zones of Tabonuco (<600 m above sea level), Colorado (600-900 m), Dwarf (>900 m), and Palm forest are determined by environmental gradients. However, over the past 60-100 years, forest extent, cover, and type have been transformed: in 1936, 40% of the LEF was unforested or secondary forest and <50% had continuous canopy (>80% cover); in 1989, >97% was continuous forest. Secondary forest and agricultural lands in 1936 were replaced largely by Tabonuco and Colorado forest, which increased from 8% and 28% (1936) to 26% and 45% (1989). These broad-scale vegetation dynamics are best explained by a gradient of human land use, intense at low elevations and decreasing on steep, high terrain, which peaked historically around 1900, followed by a gradual decline in agriculture. GIS analysis and historical sources suggest that essentially all of the LEF was affected by human activity and that Tabonuco forest, which is the focus of LTER research, has been most substantially altered and is largely of secondary origin. Rapid reforestation following agricultural decline has obscured much of the past land use and confirms the resiliency of some tropical forests to intensive human disturbance. Impacts of earlier hurricanes (e.g., in 1928 and 1932), although not evident in the broad forest pattern in 1936, may be significant in explaining the distributions of Colorado and Palm forest. Damage from Hurricane Hugo in 1989 indicates that natural disturbance is increasingly important as land use declines and forest cover and height increase. However, this study and post-Hugo studies emphasize that land use legacies are long-lasting and need to be considered in modern ecological studies and natural resource management. The subtle, although persistent, effects of historical human activities may have profound consequences for modern forest ecosystems in the tropics.

Frangi, J.L.; Lugo, A.E. 1991. Hurricane Damage to a Flood Plain Forest in the Luquillo Mountains of Puerto Rico. Biotropica. 23(4a): 324-335.
https://doi.org/10.2307/2388248
Download: https://www.fs.usda.gov/research/treesearch/66362

Hurricane Hugo caused low to moderate damage to a flood plain forest that was partially protected by its topographic position. Treefalls and the location of damage suggested N to NW wind direction during the storm. Thirty percent of the trees, or 693 trees/ha, had some damage and 84 percent of the damage was to the canopy Most of the damage to trees was caused by direct wind impact (83%) as opposed to secondary effects (16%). Over 80 percent of the snapped, leaning, and uprooted trees were dicotyledonous. Tree mortality was only 1 percent, and most of the damage to the sierra palm *Prestoea montana* (R. Grah.) Nichols was loss of leaves. Rapid refoliation, epicormic branching, adventitious root production, resprouting, and regeneration from seed in open areas were observed nine months after the event. Ten percent of the aboveground biomass and 12-16 percent of the nutrient stocks (N, P, K, Ca, Mg) were transferred to the forest floor, mostly in the form of woody biomass and nutrient-rich leaves. Palm leaves were the dominant leaf component of necromass. Instantaneous in situ fine and coarse necromass production was 10 and 9.2 Mg/ha, respectively. Net changes in aboveground mass, N, P, K, Ca, and Mg (in percent of prehurricane value) were 8, 3, 0, 3, 12, and 1, respectively, in spite of a high rate of loss by export. The source of additional mass and nutrients were boles from upland forests that fell into and remained inside the flood plain.

Frangi, J.L.; Lugo, A.E. 1998. A Flood Plain Palm Forest in the Luquillo Mountains of Puerto Rico Five Years After Hurricane Hugo. Biotropica. 30(3): 339-348.
https://doi.org/10.1111/j.1744-7429.1998.tb00069.x
Download: https://www.fs.usda.gov/research/treesearch/66363

Long-term studies are needed to understand the dynamics of tropical forests, particularly those subject to periodic disturbances such as hurricanes. We studied a flood plain *Prestoea montana* palm forest in the Luquillo Mountains of Puerto Rico over a 15-yr period (1980-1995), which included the passage of Hurricane Hugo in September 1989. The passage of the hurricane caused the dominant species to become more dominant and created low instantaneous tree mortality (1% of stems) and reductions in tree biomass (-16 Mg/ha/yr) and density, although not in basal area. Five years after the hurricane, the palm flood plain forest had exceeded its prehurricane aboveground tree biomass, tree density, and basal area. Aboveground tree biomass accumulated at a rate of 9.2 Mg/ha/yr, 76 percent of which was due to palms. Before the hurricane this rate was on the order of 3 Mg/ha/yr. Forest floor litter

decreased to prehurricane levels (6.7 Mg/ha), within 5 yr, mostly due to the disappearance of woody litter. Thirteen tree species not represented in the canopy entered the forest by regeneration, and 2 species suffered almost 20 percent/yr mortality over a 5-yr period after the storm (floodplain average of 2%/yr). Delayed tree mortality was twice as high as instantaneous tree mortality after the storm and affected dicotyledonous trees more than it did palms. Regeneration of dicotyledonous trees, palms, and tree ferns was influenced by a combination of factors including hydroperiod, light, and space. Redundancy Data Analysis showed that the area near the river channel was the most favorable for plant regeneration. Palm regeneration was higher in locations with longer hydroperiods, while regeneration of dicotyledonous trees was higher in areas with low risk of flooding. This study shows how a periodic disturbance provides long-term opportunities for species invasions and long-term ecosystem response at the patch scale of <1 ha.

Fu, S.; Rodríguez Pedraza, C.; Lugo, A.E. 1996. A Twelve-Year Comparison of Stand Changes in a Mahogany Plantation and a Paired Natural Forest of Similar Age. Biotropica. 28(4a): 515-524. https://doi.org/10.2307/2389093
Download: https://www.fs.usda.gov/treesearch/pubs/30478

We compared forest structure over a 12 yr period (1982-1994) that included measurements before and after a severe hurricane in two forests: a 64 yr old *Swietenia macrophylla* tree plantation and a paired natural forest of similar age in a subtropical wet forest life zone at 200 m elevation in Puerto Rico. We measured trees 2 4 cm diameter at breast height in a 40 x 50 m plot at each forest type. The natural forest had lower total tree height (8.8 vs. 10.2 m in 1984), and greater basal area (35.7 vs. 28.5 m2/ha in 1989) and tree density (1525 vs. 969 trees/ha in 1989) than the plantation. Rates of tree mortality and ingrowth to the >= 4 cm diameter class were higher in the plantation than in the natural forest. Both forest types exhibited the same rate of change in these structural parameters before and after Hurricane Hugo. However, Hurricane Hugo caused a greater reduction in the rate of change of tree density and basal area of the plantation than it did in the natural forest. After the hurricane, the plantation experienced a greater fluctuation in tree species composition and tree species abundance than did the natural forest. Tree ingrowth was lower than tree mortality in both stands. By 1994, all measured rates of change were at pre-hurricane levels. The species composition and structural changes required to make the plantation more productive in terms of stemwood biomass appear to make the plantation more vulnerable to hurricane wind effects and this in turn causes greater rates of change in species composition, tree mortality, and tree ingrowth during the initial phase following the disturbance.

Gannon, M.R.; Willig, M.R. 1994. The Effects of Hurricane Hugo on Bats of the Luquillo Experimental Forest of Puerto Rico. Biotropica. 26(3): 320-331. https://doi.org/10.2307/2388854

Natural disturbances can have large effects on ecosystem structure and function depending on their scale, intensity, and frequency. On 18 September 1989 Hurricane Hugo struck Puerto Rico, with the eye of the hurricane passing within 10 km of the Luquillo Experimental Forest. This provided a rare opportunity to evaluate the effects of an infrequent but large scale and high intensity disturbance on tropical bat species. Data on demographic parameters of three common phyllostomid bats (*Artibeus jamaicensis*, *Stenoderma rufum*, and *Monophyllus redmani*) were examined for three years prior and three years after the hurricane. Population levels as estimated by captures per net hour of all three species were affected by Hurricane Hugo. Populations of A. *jamaicensis* and M. *redmani* returned to predisturbance levels within two years. In contrast, population levels of S. *rufum* declined to about 30 percent of prehurricane levels and have not recovered after three years. Moreover, telemetry data indicate that foraging and home range size expanded to encompass an area approximately five times larger than its prehurricane size. The cost of foraging, in terms of time and energy, may be considerably elevated over prehurricane scenarios. In fact, a significant change in the age structure of the population (juvenile individuals have been absent from the population since Hurricane Hugo) as well as significant decline in the percent of reproductively active females indicate a failure to reproduce in the posthurricane environment.

González, G.; Lodge, J.D.; Richardson, B.A. [and other]. 2014. A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. Forest Ecology and Management. 332: 32-46. https://doi.org/10.1016/j.foreco.2014.06.024 Download: https://www.fs.usda.gov/treesearch/pubs/46657

In this study, we used a replicated factorial design to separate the individual and interacting effects of two main components of a severe hurricane – canopy opening and green debris deposition on leaf litter decay in the tabonuco forest in the Luquillo Mountains of Puerto Rico. We quantify changes in percent mass remaining (PMR), the concentration and absolute amounts of various chemical elements using fresh (green) and senesced leaf litter contained in litterbags of two different mesh sizes. Mass loss was significantly slowed by canopy trimming. There was no significant effect of debris treatment on the PMR of the litter. Canopy trimming increased the percent of initial N, Al, Ca, Fe, and Mg remaining and decreased the percent of initial Mn remaining compared with not trimmed plots. Debris addition increased the percent of initial N and P remaining and decreased the percent of initial Al, and Fe

remaining in the decomposing litter compared to no debris added plots. Of the elements studied, only Al and Fe accumulated above 100% of initial. Accumulation of Al and Fe in the canopy trimmed and no debris plots is most likely dominated by the adsorption of these ions onto the surfaces of the decaying litter. Overall, P showed a rapid initial loss during the first 0.2 yr followed by steady loss. Nitrogen was lost steadily from leaf litter. The PMR of fresh and senesced litter was significantly affected by mesh size, with a higher mass remaining in small mesh bags. Fresh litter decayed faster than senesced litter; following patterns of initial N and P concentrations (higher in the former litter type). We found a significantly negative correlation between the Margalef index of diversity for the litter arthropods contained in the litterbags and the PMR, suggesting functional complexity is an important determinant of decay in this forest. Our results imply hurricanes can differentially impact litter decomposition and associated nutrient release via canopy opening and litter inputs.

Gregory, F.A.; Sabat, A.M. 1996. The Effect of Hurricane Disturbance on the Fecundity of Sierra Palms (*Prestoea montana*). Bios. 67(3): 135-139.
https://www.jstor.org/stable/4608377

Hurricanes are a major natural disturbance affecting Caribbean forests. For example, hurricane Hugo caused a 6 to 60-fold increase in gap area in the Luquillo Mountains, Puerto Rico. Gaps have different light, nutrient, soil, and humidity levels as compared to close canopy sites. Thus, hurricanes can create a very heterogeneous environment in terms of the resources needed by plants. The objective of this study was to assess the effect of canopy disturbance on the fruit production of sierra palms (*Prestoea montana*, Palmae) in the Luquillo Mountains, Puerto Rico. Forty-three sierra palms at sites that differed in the degree of hurricane damage to the forest canopy were selected for the study. Stem height and diameter, number of fronds, percent of crown shaded, fruit production, and floral sex ratio were measured on each individual for 2.5 years. Fruit production varied greatly among individuals. Percent of crown shaded and number of fronds explained 41.3% of the observed variance in fruit production. Palms in more exposed areas and those with more fronds tended to produce relatively more female flowers (sierra palms produced male and female unisexual flowers) and fruits than those in less disturbed sites. This demonstrates that hurricanes can have a positive effect on the average fecundity of sierra palms.

Gutiérrez del Arroyo, O.; Silver, W.L. 2018. Disentangling the long-term effects of disturbance on soil biogeochemistry in a wet tropical forest ecosystem. Global Change Biology. 24: 1673-1684. https://doi.org/10.1111/gcb.14027
Download: https://www.fs.usda.gov/research/treesearch/66364

Climate change is increasing the intensity of severe tropical storms and cyclones (also referred to as hurricanes or typhoons), with major implications for tropical forest structure and function. These changes in disturbance regime are likely to play an important role in regulating ecosystem carbon (C) and nutrient dynamics in tropical and subtropical forests. Canopy opening and debris deposition resulting from severe storms have complex and interacting effects on ecosystem biogeochemistry. Disentangling these complex effects will be critical to better understand the long-term implications of climate change on ecosystem C and nutrient dynamics. In this study, we used a well-replicated, long-term (10 years) canopy and debris manipulation experiment in a wet tropical forest to determine the separate and combined effects of canopy opening and debris deposition on soil C and nutrients throughout the soil profile (1 m). Debris deposition alone resulted in higher soil C and N concentrations, both at the surface (0–10 cm) and at depth (50–80 cm). Concentrations of NaOH-organic P also increased significantly in the debris deposition only treatment (20–90 cm depth), as did NaOH-total P (20–50 cm depth). Canopy opening, both with and without debris deposition, significantly increased NaOH-inorganic P concentrations from 70 to 90 cm depth. Soil iron concentrations were a strong predictor of both C and P patterns throughout the soil profile. Our results demonstrate that both surface- and subsoils have the potential to significantly increase C and nutrient storage a decade after the sudden deposition of disturbance-related organic debris. Our results also show that these effects may be partially offset by rapid decomposition and decreases in litterfall associated with canopy opening. The significant effects of debris deposition on soil C and nutrient concentrations at depth (>50 cm), suggest that deep soils are more dynamic than previously believed, and can serve as sinks of C and nutrients derived from disturbance-induced pulses of organic matter inputs.

Gutiérrez-Fonseca, P.E.; Pringle, C.M.; Ramírez, A. [and others]. 2023. Hurricane disturbance drives trophic changes in neotropical mountain stream food webs. Ecology. e4202. https://doi.org/10.1002/ecy.4202
Download: https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.4202

Food webs are complex ecological networks that reveal species interactions and energy flow in ecosystems. Prevailing ecological knowledge on forested streams suggests that their food webs are based on allochthonous carbon, driven by a constant supply of organic matter from adjacent vegetation and limited primary production due to low light conditions. Extreme climatic disturbances can disrupt these natural ecosystem dynamics by altering resource availability, which leads to changes in food web structure and functioning. Here, we quantify the response of stream food webs to two major hurricanes (Irma and Maria, Category 5 and 4, respectively) that struck Puerto Rico in September 2017. Within two tropical forested streams

(first and second order), we collected ecosystem and food web data 6 months prior to the hurricanes and 2, 9, and 18 months afterward. We assessed the structural (e.g., canopy) and hydrological (e.g., discharge) characteristics of the ecosystem and monitored changes in basal resources (i.e., algae, biofilm, and leaf litter), consumers (e.g., aquatic invertebrates, riparian consumers), and applied Layman's community-wide metrics using the isotopic composition of C-13 and N-15. Continuous stream discharge measurements indicated that the hurricanes did not cause an extreme hydrological event. However, the sixfold increase in canopy openness and associated changes in litter input appeared to trigger an increase in primary production. These food webs were primarily based on terrestrially derived carbon before the hurricanes, but most taxa (including Atya and Xiphocaris shrimp, the consumers with highest biomass) shifted their food source to autochthonous carbon within 2 months of the hurricanes. We also found evidence that the hurricanes dramatically altered the structure of the food web, resulting in shorter (i.e., smaller food-chain length), narrower (i.e., lower diversity of carbon sources) food webs, as well as increased trophic species packing. This study demonstrates how hurricane disturbance can alter stream food webs, changing the trophic base from allochthonous to autochthonous resources via changes in the physical environment (i.e., canopy defoliation). As hurricanes become more frequent and severe due to climate change, our findings greatly contribute to our understanding of the mechanisms that maintain forested stream trophic interactions amidst global change.

Guzmán-Grajales, S.M.; Walker, L.R. 1991. Differential Seedling Responses to Litter After Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. Biotropica. 23(4a): 407-413. https://doi.org/10.2307/2388259

We studied the dynamics of the seedling community in the Luquillo Experimental Forest during one year following Hurricane Hugo, to look at the effect of three litter treatments (continuous litter removal, unaltered litter quantity [control] and continuous litter addition), on seedling emergence, growth, density, and mortality. Total seedling densities (for both newly emerged and established seedlings) were highest in the litter removal treatment, suggesting that litter is a major constraint to recruitment of seedlings. However, species differed in their responses to the three treatments: species characteristic of early succession (*Chionanthus domingensis* and *Cecropia schreberiana ex. C. peltata*) were densest in the litter removal treatment, while densities of species characteristic of late succession either did not increase (*Sloanea berteriana*) or declined (*Dacryodes excelsa*) in the litter removal treatment. Height growth was lowest and mortality generally highest for seedlings in the litter removal treatment. Variability in species responses to litter after the hurricane may lead to changes in the species composition of the forest.

Hall, J.; Muscarella, R.; Quebbeman, A. [and others]. 2020. Hurricane-Induced Rainfall is a Stronger Predictor of Tropical Forest Damage in Puerto Rico Than Maximum Wind Speeds. Scientific Reports. 10: 4318. https://doi.org/10.1038/s41598-020-61164-2 Download: https://www.nature.com/articles/s41598-020-61164-2#:~:text=Using%20field%20and%20remote%20sensing,damage%20than%20maximum%20wind%20speeds

Projected increases in cyclonic storm intensity under a warming climate will have profound effects on forests, potentially changing these ecosystems from carbon sinks to sources. Forecasting storm impacts on these ecosystems requires consideration of risk factors associated with storm meteorology, landscape structure, and forest attributes. Here we evaluate risk factors associated with damage severity caused by Hurricanes María and Irma across Puerto Rican forests. Using field and remote sensing data, total forest aboveground biomass (AGB) lost to the storms was estimated at 10.44 (±2.33) Tg, ca. 23% of island-wide pre-hurricane forest AGB. Storm-related rainfall was a stronger predictor of forest damage than maximum wind speeds. Soil water storage capacity was also an important risk factor, corroborating the influence of rainfall on forest damage. Expected increases of 20% in hurricane-associated rainfall in the North Atlantic highlight the need to consider how such shifts, together with high speed winds, will affect terrestrial ecosystems.

Hall, C.A.S.; Taylor, M.R.; Everham, E. 1992. A geographically-based ecosystem model and its application to the carbon balance of the Luquillo Forest, Puerto Rico. Water, Air, and Soil Pollution. 64: 385-404. https://doi.org/10.1007/BF00477112

We have developed a geography-based computer model of the Bisley Experimental Watershed ecosystem that simulates basic forest dynamics as a function of meteorological inputs and hydrologic simulation, as influenced by topography, soils, land use, and cover. The model is parameterized based on steady slate levels of, and hurricane impacts on, biomass, necromass and rate processes of the tabonuco forest, and is stable over decades. Over a 60 yr simulation (without hurricanes) leaf biomass remains approximately constant and woody biomass of those regions not having severe sunlight, moisture, or nutrient limitations increases slowly in agreement with observations. Necromass decreases slowly. Small quantities of C leave the ecosystem in stream water, especially during large rain events. When topographically-sensitive hurricane impacts are included, leaf and woody biomass are converted to necromass. In the model the recovery of the watersheds' hydrology, leaf and woody biomass, and necromass are consistent with field observations. We used this model to simulate the C dynamics of the forest over centurics using empirical values and found that (his forest acted to pump C from the atmosphere to the ocean at a rate of about 90 kg ha^{-1} yr^{-1}.

Halleck, L.F.; Sharpe, J.M.; Zou, X. 2004. Understory fern responses to post-hurricane fertilization and debris removal in a Puerto Rican rain forest. Journal of Tropical Ecology. 20: 173-181. https://doi.org/10.1017/S026646740300124X

Controls over net primary productivity are the subject of a long-term experiment within a lowland subtropical wet forest in the Luquillo mountains of Puerto Rico. Responses of the fern community to fertilization and debris-removal treatments and to monitoring activities were assessed 6 y after the experiment began in October 1989, just after the passage of Hurricane Hugo. Negative fern responses to fertilization included a qualitative change in species composition and a 13-fold reduction in density compared with controls. Plants were smaller and spore production rates were lower. Debris removal reduced the number of species and increased the proportion of terrestrial species. Density of *Nephrolepis rivularis* individuals in debris-removal plots was only 5% that of control levels while abundance of *Thelypteris deltoidea* nearly doubled. Buffer-zone fern density was 36% greater than and per cent of leaves damaged was half that of the monitored zones. The magnitude of the responses of ferns to experimental treatments and to monitoring effects suggest that they may be good early indicators of change in a tropical forest.

Haney, C.; Wunderle, J.M.; Arendt, W.J. 1991. Some initial effects of Hurricane Hugo on endangered and endemic species off west Indian birds. American Birds. 45(2): 234-236.
Download: https://www.fs.usda.gov/treesearch/pubs/61449

Heartsill Scalley, T. 2017. Insights on Forest Structure and Composition from Long-Term Research in the Luquillo Mountains. Forests. 8(6): 204. https://doi.org/10.3390/f8060204
Download: https://www.fs.usda.gov/treesearch/pubs/54419

The science of ecology fundamentally aims to understand species and their relation to the environment. At sites where hurricane disturbance is part of the environmental context, permanent forest plots are critical to understand ecological vegetation dynamics through time. An overview of forest structure and species composition from two of the longest continuously measured tropical forest plots is presented. Long-term measurements, 72 years at the leeward site, and 25 years at windward site, of stem density are similar to initial and pre-hurricane values at both sites. For 10 years post-hurricane Hugo (1989), stem density increased at both sites. Following that increase period, stem density has remained at 1400 to 1600 stems/ha in the leeward site, and at 1200 stems/ha in the windward site. The forests had similar basal area values before hurricane Hugo in 1989, but these sites are following different patterns of basal area accumulation. The leeward forest site continues to accumulate and increase basal

area with each successive measurement, currently above 50 m²/ha. The windward forest site maintains its basal area values close to an asymptote of 35 m²/ha. Currently, the most abundant species at both sites is the sierra palm. Ordinations to explore variation in tree species composition through time present the leeward site with a trajectory of directional change, while at the windward site, the composition of species seems to be converging to pre-hurricane conditions. The observed differences in forest structure and composition from sites differently affected by hurricane disturbance provide insight into how particular forest characteristics respond at shorter or longer time scales in relation to previous site conditions and intensity of disturbance effects.

Heartsill Scalley, T.; Scatena, F.N.; Lugo, A.E. [and others]. 2010. Changes in Structure, Composition, and Nutrients During 15 Years of Hurricane-induced Succession in a Subtropical Wet Forest in Puerto Rico. Biotropica. 42(4): 455-463.
https://doi.org/10.1111/j.1744-7429.2009.00609.x
Download: https://www.fs.usda.gov/treesearch/pubs/36542

The trajectory of hurricane-induced succession was evaluated in a network of forest plots measured immediately before and 3 mo, 5, 10, and 15 yr after the direct impact of a Category 4 hurricane. Comparisons of forest structure, composition, and aboveground nutrients pools were made through time, and between species, life-history groups and geomorphic settings. The hurricane reduced aboveground biomass by 50 percent, causing an immediate decrease in stem density and diversity indices among all geomorphic settings. After 15 yr, basal area and aboveground biomass returned to pre-hurricane levels, while species richness, diversity indices, and stem densities exceeded pre-hurricane levels. Differences in species composition among geomorphic settings had not returned after 15 yr but differences in stem densities and structure were beginning to emerge. Significant differences were observed in the nutrient concentration of the three species that comprised the most aboveground biomass, and between species categorized as secondary high-light species and primary, low-light species. Species whose abundance was negatively correlated with the mature forest dominant also had distinct nutrient concentrations. When total aboveground nutrient pools were compared over time, differences in leaf nutrients among species were hidden by similarities in wood nutrient concentrations and the biomass dominance of a few species. The observed successional trajectory indicates that changes in species composition contributed to fast recovery of aboveground biomass and nutrient pools, while the influence of geomorphic setting on species composition occurs at time scales >15yr of succession.

Heartsill Scalley, T.; Scatena, F.N.; Moya, S. [and other]. 2012. Long-term dynamics of organic matter and elements exported as coarse particulates from two Caribbean montane watersheds. Journal of Tropical Ecology. 28(2): 127-139.
https://doi.org/10.1017/S0266467411000733
Download: https://www.fs.usda.gov/treesearch/pubs/41610

In heterotrophic streams the retention and export of coarse particulate organic matter and associated elements are fundamental biogeochemical processes that influence water quality, food webs and the structural complexity of forested headwater streams. Nevertheless, few studies have documented the quantity and quality of exported organic matter over multiple years and under a range of conditions that includes both droughts and hurricanes. This study quantifies the export of coarse particulate organic matter (CPOM, > 12.7 mm), over 18 y in two headwater streams in north-east Puerto Rico. Daily exports ranged from 0 to over 170 g ha^{-1} d^{-1} and averaged 7.39 g ha^{-1} d^{-1} , with similar amounts coming from leaves (3.5 g ha^{-1} d^{-1}) and wood (3.2 g ha^{-1} d^{-1}). Export of coarse particulate organic carbon was 3.0 g ha^{-1} d^{-1} which constitutes only 1.32% of carbon exports. Most litter falling into the streams was processed in place as only 2.3% of the leaf litter falling directly into these perennial channels was exported as CPOM. On average, 6 wk y^{-1} had no exports while events transporting more than 10 g ha^{-1} d^{-1} occurred every 2.8 mo. Instead of a single annual pulse as observed in deciduous systems, there were annual peaks in CPOM exports during May and September and less export during the drier period from December to February. Ratios of C:N in the exported material were highest in the driest month and lowest during rainy months, while leaf fluxes for nitrogen, phosphorus and calcium were highest in rainy months and lowest during February. Although median daily exports and exports during low-and base-flow periods were similar before and after Hugo, after 16 y exports during moderate and high-flow periods were still less than those in the 2 y prior to the hurricane. Our observations indicate a system with high rates of internal processing that quickly returns to median daily conditions following hurricanes but requires several decades for storm-flow exports to return to pre-disturbance conditions and indicates that the long-term pattern of CPOM export is associated with the level of maturity of watershed vegetation.

Heartsill Scalley, T.; Scatena, F.N.; Estrada, C. [and others]. 2007. Disturbance and long-term patterns of rainfall and throughfall nutrients fluxes in a subtropical wet forest in Puerto Rico. Journal of Hidrology. 333(2): 472-485.
https://doi.org/10.1016/j.jhydrol.2006.09.019
Download: https://www.fs.usda.gov/treesearch/pubs/30013

Nutrient fluxes in rainfall and throughfall were measured weekly in a mature subtropical wet forest in NE Puerto Rico over a 15-year period that included the effects of 10 named

tropical storms, several prolonged dry periods, and volcanic activity in the region. Mean annual rainfall and throughfall were 3482 and 2131 mm yr^{-1}, respectively. Average annual rainfall and throughfall fluxes of K, Ca, Mg, Cl, Na, and SO_4–S were similar but somewhat larger than those reported for most tropical forests. Rainfall inputs of nitrogen were comparatively low and reflect the relative isolation of the airshed. More constituents had seasonal differences in rainfall fluxes (6 out of 12) than throughfall fluxes (4 out of 12) and all volume weighted throughfall enrichment ratios calculated for the 15-year period were greater than one. However, median weekly enrichment ratios were less than 1 for sea salts and dissolved organic carbon, between 1 and 2 for Mg, Ca, SiO_2 and SO_4–S, and greater than 10 for NH_4–N, PO_4–P, and K. Droughts tended to reduce enrichment ratios of cations and sea-salts, but increased enrichment ratios of NH_4–N, PO_4–P, and K. In the weeks following hurricanes and tropical storms, relative throughfall tended to be higher and enrichment ratios tended to be lower. Saharan dust and the activity of Caribbean volcanoes can also be detected in the time series. Nevertheless, the impacts of particular events are variable and modified by the magnitude of the event, the pre- and post-event rainfall, and the time since the previous event. Rainfall, throughfall, rainfall pH, and rainfall fluxes of seven constituents had decreasing trends over the 15-year period. However, these decreases were small, less than inter-annual and annual variations, and not considered to be ecologically significant. These long-term observations indicate that physical and biological processes associated with water passing through the canopy act to buffer internal nutrient cycles from inter-annual and seasonal variations in rainfall inputs.

Helmer, E.H.; Shannon, K.; Marcano-Vega, H. [and others]. 2023. Multiscale predictors of small tree survival across a heterogeneous tropical landscape. PLoS ONE. 18(3): e0280322. https://doi.org/10.1371/journal.pone.0280322
Download: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0280322

Uncertainties about controls on tree mortality make forest responses to land-use and climate change difficult to predict. We tracked biomass of tree functional groups in tropical forest inventories across Puerto Rico and the U.S. Virgin Islands, and with random forests we ranked 86 potential predictors of small tree survival (young or mature stems 2.5–12.6 cm diameter at breast height). Forests span dry to cloud forests, range in age, geology and past land use and experienced severe drought and storms. When excluding species as a predictor, top predictors are tree crown ratio and height, two to three species traits and stand to regional factors reflecting local disturbance and the system state (widespread recovery, drought, hurricanes). Native species, and species with denser wood, taller maximum height, or medium typical height survive longer, but short trees and species survive hurricanes better.

Trees survive longer in older stands and with less disturbed canopies, harsher geoclimates (dry, edaphically dry, *e.g.*, serpentine substrates, and highest-elevation cloud forest), or in intervals removed from hurricanes. Satellite image phenology and bands, even from past decades, are top predictors, being sensitive to vegetation type and disturbance. Covariation between stand-level species traits and geoclimate, disturbance and neighboring species types may explain why most neighbor variables, including introduced vs. native species, had low or no importance, despite univariate correlations with survival. As forests recovered from a hurricane in 1998 and earlier deforestation, small trees of introduced species, which on average have lighter wood, died at twice the rate of natives. After hurricanes in 2017, the total biomass of trees ≥12.7 cm dbh of the introduced species *Spathodea campanulata* spiked, suggesting that more frequent hurricanes might perpetuate this light-wooded species commonness. If hurricane recovery favors light-wooded species while drought favors others, climate change influences on forest composition and ecosystem services may depend on the frequency and severity of extreme climate events.

Hernández-Muñiz, R.M.; Meléndez-Ackerman, E.J.; Tremblay, R.L. [and other]. 2021. Short-term effects of Hurricane María on populations size and individual survival in *Lepanthes eltoroensis* (Orchidaceae) at the Luquillo Experimental Forest, Puerto Rico. Acta Científica. 32(1-3): 23-32.
Download: https://www.fs.usda.gov/research/treesearch/66365

Plants endemic to the Caribbean región have evolved in response to hurricanes. These natural phenomena appear to be more frequent and more intense in the Caribbean region, which requires the study and understanding of their influence on responses by these plants – particularly if rare and with limited geographical distribution within ther region – as as a priority for conservation. We took advantage of long-term monitoring studies at the Luquillo Esperimental Forest/El Yunque National Forest in Puerto Rico to evaluate the short-term changes in population size and the distribution of life stages of *Lepanthes eltoroensis*, a species listed as endangered under the Endangered Species Acto f 1973, in response to Hurricane María. We expected there to be reductions in overall population size, and also the plants of smaller developlental stages (seedlings and juveniles) would be more affected by hurricanes compared to larger plants (i.e., adults). To examine these predictors, we conducted a rapid assesment (six-month after the storm) of inventoried subpopulations of this species, and that also are georeferenced before the 2017-hurricane season. This information is valuable for efective management and conservation for this species.

Hogan, J.A.; Mayorquín, S.; Rice, K. [and others]. 2017. Liana dynamics reflect land-use history and hurricane response in a Puerto Rican forest. Journal of Tropical Ecology. 33(2): 155-164. https://doi.org/10.1017/S0266467417000049

We studied lianas in a subtropical wet forest in Puerto Rico to understand how hurricane impacts and past human land-uses interact to affect liana dynamics over a 14-year period. We compared a high-intensity land-use area, where the forest that had been cleared, and used for subsistence agriculture before being abandoned in 1934 then regrew to a low-intensity land-use area, in which there had been only some selective experimental logging by the USDA Forest Service in the 1940s. Prior to our study, both areas were strongly affected by Hurricane Hugo in 1989, and again damaged to a lesser degree by Hurricane Georges in 1998, increasing canopy openness and subsequently increasing tree stem densities. Between 2001 and 2015, changes in the light environment and the recovery of forest structure resulted in roughly a 50% reduction in tree stem densities in the high-intensity land-use area, as recruited saplings naturally thinned. In this area, liana abundance increased by 103%, liana biomass tripled, and occupancy of trees by lianas grew by nearly 50%. In the low-intensity land-use area, juvenile stem densities were stable, and resultantly liana abundance only increased by 33%, liana biomass rose 39%, and the occupancy of trees was constant. Liana flower and fruit production increased over the 14-year interval, and these increases were much greater in the high-intensity land-use quadrats. Results of this study do show how rapid forest tree successional dynamics coincide with liana increases, but the confounding of hurricane effects of disturbance at our site, prevent us from asserting that the increases in liana density and biomass can be attributed to the same causes as those in forests elsewhere in the Neotropics.

Hogan, J.A.; Sharpe, J.M.; Van Beusekon, A. [and others]. 2022. Solar radiation and soil moisture drive tropical forest understory responses to experimental and natural hurricanes. Ecosphere. 33: e4150. https://doi.org/10.1002/ecs2.4150
Download: https://www.fs.usda.gov/treesearch/pubs/64516

Tropical forest understory regeneration occurs rapidly after disturbance with compositional trajectories that depend on species availability and environmental conditions. To predict future tropical forest regeneration dynamics, we need a deeper understanding of how pulse disturbance events, like hurricanes, interact with environmental variability to affect understory demography and composition. We examined fern and sapling mortality, recruitment, and community composition in relation to solar radiation and soil moisture using 17 years of forest dynamics data (2003-2019) from the Canopy Trimming Experiment in the Luquillo Experimental Forest, Puerto Rico. Solar radiation increased 150% and soil moisture increased 40% following canopy trimming of experimental plots relative to control plots. All plots were disturbed in 2017 by Hurricanes Irma and Maria, so experimentally

trimmed plots presented the opportunity to study the effects of multiple hurricanes, while control plots isolated the effects of a single natural hurricane. Recruitment rates maximized at 0.14 in dividuals/plot/month for ferns and 0.20 stems/plot/month for saplings. Recruitment and mortality were distributed more evenly over the 17 years of monitoring in experimentally trimmed plots than in control plots; however, following Hurricane Maria demographic rates substantially increased in control plots only. In experimentally trimmed plots, the largest community compositional shifts occurred as a result of the trimming events, and compositional changes were greatest for control plots after Hurricane Maria in 2017. Pioneer tree and fern species increased in abundance in response to both simulated and natural hurricanes. Following Hurricane Maria, two dominant pioneer species, *Cyathea arborea* and *Cecropia schreberiana*, recruited abundantly, but only in control plots. In trimmed plots, increased solar radiation and soil moisture shifted understory species composition steadily toward pioneer and secondary-successional species, with soil moisture interacting strongly with canopy trimming. Thus, both solar radiation and soil moisture are environmental drivers affecting pioneer species recruitment following disturbance, which interact with canopy opening following hurricanes. Our results suggest that if hurricane disturbances increase in frequency and severity, as suggested by climate change predictions, the understory regeneration of late-successional species, such as *Manilkara bidentata* and *Sloanea berteroana*, which prefer deeper shade and slightly drier soil microsites, may become imperiled.

Hogan, J.A.; Zimmerman, J.; Uriarte. M. [and others]. 2016. Land-use history augments environment-plant community relationship strength in a Puerto Rican wet forest. Journal of Ecology. 104(5): 1466-1477. https://doi.org/10.1111/1365-2745.12608
Download: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12608

(1) Environmental heterogeneity influences the species composition of tropical forests, with implications for patterns of diversity and species coexistence in these hyperdiverse communities. Many studies have examined how variability in soil nutrients and topography influence plant community composition, with differing results. None have quantified the relative contribution of environmental heterogeneity versus endogenous processes to variability in forest community composition over time and with respect to successional recovery. (2) Using five consecutive trees censuses of a forest plot in Puerto Rico, conducted between 1990 and 2011, we evaluated the influence of edaphic and topographic variability on community composition. The plot has a well-documented land-use history and is subject to periodic hurricane disturbance. Using multiple canonical distance-based redundancy analyses, we studied how spatial heterogeneity in soil nutrients and topography structure community composition over time, as the forest recovers from long-term land-use effects and two major hurricanes in 1989 and 1998. (3) For the entire plot, spatial variables (principle

coordinates of neighbourhood matrices), representing the autocorrelation of tree species in the community, explained the majority (49–57%) of the variability in tree community composition. The explanatory power of spatial variables decreased over time, as forest structure recovered from hurricane damage and the stems in the understorey died. Soil nutrients and topography, collectively, explained a moderate portion (33–37%) of the species compositional variation and were slightly more robust in explaining compositional differences in areas of more intense past land use. (4) Areas of less-intense past land use showed weaker community–environmental trends overall, illustrating a tendency for stronger resource competition (i.e. light, water and soil nutrients) between species in these areas. This illustrates how environmental–plant community interactions are strengthened by the lasting effects of human land-use legacies, which persist for decades to centuries. (5) Synthesis. Our findings confirm past land use to be a fundamental driver of the structure and composition of secondary forests through its impacts on the tree community, the abiotic terrestrial environment and their interaction. Since the extent of second-growth tropical forests continues to increase, our findings highlight the importance of understanding the processes that determine the rate and nature of their succession.

Hogan, J.A.; Zimmerman, J.K.; Thompson, J. [and others]. 2018. The Frequency of Cyclonic Wind Storms Shapes Tropical Forest Dynamism and Functional Trait Dispersion. Forests. 9(7): 404. https://doi.org/10.3390/f9070404
Download: https://www.mdpi.com/1999-4907/9/7/404

As cyclonic wind storms (hurricanes and typhoons) increase in frequency and intensity with climate change, it is important to understand their effects on the populations and communities of tropical trees they impact. Using tree demographic data from four large, tropical forest dynamics plots that differ in cyclonic storm frequency, we compare tree population and community dynamics. Additionally, we assess the effect of cyclonic storms on three functional traits, specific leaf area, wood density, and tree height of the dynamic tree assemblages. Mortality, growth and recruitment rates and the intrinsic rates of population growth of species differed across the plots, and were most dynamic, especially for stems 1–2 cm in diameter, at the plot which had an intermediate level of cyclonic storm frequency. Functional assemblages of species had the greatest degree of temporal variation in relation to disturbance, as measured by the change in functional divergence for the two plots with more intermediate cyclonic storm recurrence. Therefore, cyclonic storms affecting these plots generally have a greater effect on forest composition and dynamism than comparable cyclonic storms do on the plot which experiences cyclonic storms more frequently. Thus, we provide some evidence that community-wide demographic resistance to cyclonic storms is generally lower at an intermediate frequency of storms. While cyclonic storm strength and timing are

important determinants of the within forest variation in tree dynamics and functional trait assemblages, we also show that cyclonic storm timing and frequency shapes tropical forest dynamics and functional composition across forests. We conclude that, over a given time interval, sites with intermediate levels of damaging cyclonic wind disturbance express a greater potential for life-history variation in the forest community, when compared to sites with less or more frequent disturbance.

Hogan, J.A.; Zimmerman, J.; Thompson, J. [and others]. 2016. The interaction of land-use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change. Ecosphere. 7(8): e01405. https://doi.org/10.1002/ecs2.1405
Download: https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.1405

Disturbance shapes plant communities over a wide variety of spatial and temporal scales. How natural and anthropogenic disturbance interact to shape ecological communities is highly variable and begs a greater understanding. We used five censuses spanning the years 1990–2011 from the 16-ha Luquillo Forest Dynamics Plot (LFDP) in northeast Puerto Rico to investigate the interplay of human land-use legacies dating to the early 20th century and two recent hurricanes (Hugo, 1989 and Georges, 1998). The LFDP is a landscape mosaic comprised of an area of mature subtropical wet forest and three areas of secondary forest with differing past land-use intensities. We examined the degree to which hurricane disturbance–effect and subsequent community recovery varied across past land-use classes. We expected areas with greater intensity of human land use to be more affected by hurricane disturbance therefore exhibiting greater initial damage and longer successional recovery times. Structurally, areas of secondary forest contained smaller trees than old-growth areas; hurricanes caused widespread recruitment of shrubs and saplings that thinned with time since the first hurricane. Species richness of the plot declined over time, mostly due to the loss of rare species, but also due to the loss of some heliophilic, pioneer species that became abundant after the first hurricane. Species composition differed strongly between areas of secondary and mature forest, and these differences were largely constant over time, except for an increase in compositional differences following the second hurricane. An indicator species analysis attributed this pattern to the longer persistence of pioneer species in areas of greater past land-use intensity, likely due to the more open canopy in secondary forest. When secondary forest areas of differing past land-use intensity were considered separately, few species of low community rank were found as indicators. When these areas were combined, more and higher-ranked species emerged as indicators, creating ecologically meaningful indicator species combinations that better captured the broad-scale plant community response to past land use. Our findings support the idea that effects of past land use can

persist for decades to centuries following land-use abandonment, illustrating the importance of land-use legacies in shaping regenerating tropical secondary forests.

Jones, K.E.; Barlow, K.E.; Vaughan, N. [and others]. 2001. Short-term impacts of extreme environmental disturbance on the bats of Puerto Rico. Animal Conservation. 4: 59-66. https://doi.org/10.1017/S1367943001001068

The sensitivity of bat species to stochastic disturbance was investigated by exploiting the natural experiment provided by Hurricane Georges, which struck the island of Puerto Rico (Caribbean) in September 1998. Six forest habitats and three cave roost sites sampled for bats prior to the hurricane were sampled in the same way after the hurricane. Populations showed significant declines in abundance and species richness across all forest habitats sampled. Species' sensitivity to disturbance were not equal: larger species were significantly more affected by disturbance than smaller species, once the effects of phylogenetic non-independence were removed. There was some evidence that frugivorous and nectarivorous species are more affected by hurricane disturbance than insectivorous species. These findings have important implications for maintaining viable populations of species in areas that experience a high degree of environmental fluctuation.

Kennard, D.K.; Matlaga, D.; Sharpe, J. [and others]. 2020. Tropical understory herbaceous community responds more strongly to hurricane disturbance than to experimental warming. Ecology and Evolution. 10(16): 8906-8915. https://doi.org/10.1002/ece3.6589
Download: https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.6589

The effects of climate change on tropical forests may have global consequences due to the forests' high biodiversity and major role in the global carbon cycle. In this study, we document the effects of experimental warming on the abundance and composition of a tropical forest floor herbaceous plant community in the Luquillo Experimental Forest, Puerto Rico. This study was conducted within Tropical Responses to Altered Climate Experiment (TRACE) plots, which use infrared heaters under free-air, open-field conditions, to warm understory vegetation and soils + 4°C above nearby control plots. Hurricanes Irma and María damaged the heating infrastructure in the second year of warming, therefore, the study included one pretreatment year, one year of warming, and one year of hurricane response with no warming. We measured percent leaf cover of individual herbaceous species, fern population dynamics, and species richness and diversity within three warmed and three control plots. Results showed that one year of experimental warming did not significantly affect the cover of individual herbaceous species, fern population dynamics, species richness, or species

diversity. In contrast, herbaceous cover increased from 20% to 70%, bare ground decreased from 70% to 6%, and species composition shifted pre to posthurricane. The negligible effects of warming may have been due to the short duration of the warming treatment or an understory that is somewhat resistant to higher temperatures. Our results suggest that climate extremes that are predicted to increase with climate change, such as hurricanes and droughts, may cause more abrupt changes in tropical forest understories than longer-term sustained warming.

Klawinski, P.D.; Dalton, B.; Shiels, A.B. 2014. Coqui frog populations are negatively affected by canopy opening but not detritus deposition following an experimental hurricane in a tropical rainforest. Forest Ecology and Management. 332: 118-123.
https://doi.org/10.1016/j.foreco.2014.02.010
Download: https://www.fs.usda.gov/treesearch/pubs/47906

Hurricanes, cyclones, and typhoons are common disturbances in many island and coastal forests. There is a lack of understanding of the importance to forest biota of the two major physical aspects that occur simultaneously during a hurricane: canopy disturbance and detritus (debris) deposition onto the ground. Using a replicated factorial design, our study involved experimentally determining the independent and interactive effects of canopy opening and debris additions to the forest floor on densities of coqui frogs (*Eleutherodactylus coqui*). Coquies are the dominant amphibian, and second most common vertebrate species, in the Luquillo Experimental Forest (LEF), a montane, tropical rainforest in northeastern Puerto Rico that frequently experiences hurricanes. Frogs were sampled in all twelve 30 × 30 m plots at three periods prior to installing treatments (July 2003, January 2004, July 2004), and at months 1, 3, 6, and 12 post-treatment. The degree of canopy opening and amount of debris deposited onto the forest floor by our experimental treatments closely mimicked conditions resulting from Hurricane Hugo, a severe hurricane that passed over the LEF in 1989. Based on findings from past studies involving natural hurricanes in the LEF, we predicted that coqui densities would increase in response to debris additions, and decrease or remain unchanged in response to canopy disturbance. However, we found that debris deposition had no significant effect on coqui density and that the opening of the canopy was the dominant aspect affecting coqui by significantly reducing their densities. We identified several possible explanations for the decreased coqui densities in open-canopy plots, including decreased litter moisture and insect prey, and temporal and spatial scales associated with disturbance that may have influenced coqui behavior. Following natural hurricanes, and in light of our findings from experimental hurricane impacts, we expect that coquies benefit from patches of intact canopy while suffering reduced densities in open-canopy settings. Furthermore, based on our study and other experimental forest studies involving frogs, future forest practices

that remove significant canopy should probably be viewed as having an initially (up to 1 year) negative effect on the frog community.

Larsen, C.M.; Torres-Sánchez, A.J.; Concepción, I.M. 1999. Slopewash, Surface runoff and fine-litter transport in forest and landslide scars in humid-tropical steeplands, Luquillo Experimental Forest, Puerto Rico. Earth Surface Processes and Landforms. 24: 481-502.

Rainfall, slopewash (the erosion of soil particles), surface runoff and fine-litter transport steepland sites in the Luquillo Experimental Forest, Puerto Rico (18° 20' N, 65° 45' W) were measured from 1991 to 1995. Hillslopes underlain by (1) Cretaceous tuffaceous sandstone and silstone in subtropical rain (tanonuco) forest with vegetation recovering from Hurricane Hugo (1989), and (2) Tertiary quartz diorite in subtropical lower mantone wet (colorado and dwarf) forest with undisturbed forest canopy were compared to recent landslide scars. Monthly surface runoff on these very steep hillslopes (24° to 43°) was only 0·2 to 0·5 per cent of monthly rainfall. Slopewash was higher in sandy loam soils whose parent material is quartz diorite (averaging 46 g m^{-2} a^{-1}) than in silty clay loam soils derived from tuffaceous sandstone and siltstone where the average was 9 g m^{-2} a^{-1}. Annual slopewash of 100 to 349 g m^{-2} on the surfaces of two recent, small landslide scars was measured initially but slopewash decreased to only 3 to 4 g m^{-2} a^{-1} by the end of the study. The mean annual mass of fine litter (mainly leaves and twigs) transported downslope at the forested sites ranged from 5 to 8 g m^{-2} and was lower at the tabonuco forest site, where post-Hurricane Hugo recovery is still in progress. Mean annual fine-litter transport was 2·5 g m^{-2} on the two landslide scars.

Latta, S.C.; Wunderle, J.M.; Terranova, R. [and other]. 1995. An experimental study of nest predation in a subtropical wet forest following hurricane disturbance. Wilson Bulletin 107(4): 590-602. http://www.jstor.org/stable/4163596
Download: https://www.fs.usda.gov/research/treesearch/66366

We used artificial nest experiments to study rates and patterns of egg predation in subtropical wet and lower montane wet forest on the island of Puerto Rico. Levels of depredation were higher for ground nests than for elevated nests, but we found no difference in rates of egg predation between forest edge (5-50 m) and forest interior (100-250 m) nests. We quantified 25 forest vegetation variables surrounding ground and elevated, forest interior nests, and correlated nest success with these vegetation parameters. Utilizing discriminant function analysis, nest success was correctly classified in 59% of cases (for ground nests) using two vegetation variables (shrub density and vegetation in the 2.5-3.0 m foliage height class), and in 71% of cases (for elevated nests) using six vegetation variables (canopy cover, vegetation in

the 0-0.5, 0.5-1.0, 1.0-1.5, and 3.0-4.0 m foliage height classes, and Cecropia tree density). Our data suggest that the absence of an induced edge effect is the result of the creation of canopy openings and early successional vegetative associations in a matrix across the forest following hurricane disturbance in 1989. Comparative data suggest that the high rates of egg predation recorded here may be typical for insular forest habitats.

Lenart, M.T.; Falk, D.A.; Scatena, F.N. [and other]. 2010. Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico. Forest Ecology and Management. 259(6): 1076-1084. https://doi.org/10.1016/j.foreco.2009.12.014
Download: https://www.fs.usda.gov/treesearch/pubs/36578

Soil turnover by tree uprooting in primary and secondary forests on the island of Puerto Rico was measured in 42 study plots in the months immediately after the passage of a Category 3 hurricane. Trunk basal area explained 61% of the variability of mound volume and 53% of the variability of mound area. The proportion of uprooted trees, the number of uprooted trees, or the proportion of uprooted basal area explained 84–85% of the variation in hurricane-created mound area. These same variables explain 79–85% of the variation in mound volume. The study indicates that the soil turnover period from tree uprooting by Puerto Rican hurricanes is between 1600 and 4800 years. These rates are faster than soil turnover by landslides and background treefall in the same area and provide a useful age constraint on soil profile development and soil carbon sequestration in these dynamic landscapes.

Lewis, A.R. 2007. Hurricane-related vagrancy of Swainson's thrush and veery in Puerto Rico. Caribbean Journal of Science. 43(1): 150-154.
https://doi.org/10.18475/cjos.v43i1.a16

Low pressure waves that contributed to the formation of Hurricane Wilma in the western Caribbean produced westerly winds in the central Caribbean and Puerto Rico during the second week of October, 2005. On October 12 and for the following two weeks Swainson's Thrush (*Catharus ustulatus*, six locations) and Veery (*C. fuscescens*, one location) were reported from the island. These species usually migrate through Central America and the central Caribbean and appear not to have been recorded before in Puerto Rico. The hurricane season overlaps the autumnal migration. Increase in cyclonic activity with local wind direction dependent on the location of centers of low pressure may increase vagrancy.

Liegel, L.H. 1984. Assessment of hurricane rain/wind damage in *Pinus caribaea* and *Pinus oocarpa* provenance trials in Puerto Rico. Commonwealth Forestry Review. 63(1): 47-53. https://www.jstor.org/stable/42606360

In 1979 hurricane-associated heavy rains and high winds caused four distinct kinds of mechanical injury or damage in 5- and 6-year old *Pinus caribaea* and *Pinus oocarpa* provenance trails in Puerto Rico. These sites are part of the International Pine Trials sponsored by the Commonwealth Forestry Institute (CFI) in Oxford, England. Assessments at six widely separated and environmentally diverse sites across the island showed 22% toal (blow-down plus lean) damage for *P. caribaea*, 52% for *P. oocarpa*. Blown-down mortality alone averaged 2% for *P. caribaea*, 13% for *P. oocarpa*. For *P. caribaea* trails, sites with high foxtail percentage did not show greater wind breakage than sites with low foxtail percentage. Overall, windthrow and lean were both major damage categories, stem and branch breakage were minimal, and there was no defoliation. Relationships between environmental or stand variables and damage percent were generally curvilinear, not linear.

Liu, X.; Zeng, X.; Zou, X. [and others]. 2018. Litterfall Production Prior to and during Hurricanes Irma and Maria in Four Puerto Rican Forests. Forests. 9(6): 367.
https://doi.org/10.3390/f9060367
Download: https://www.mdpi.com/1999-4907/9/6/367

Hurricanes Irma and Maria struck Puerto Rico on the 6th and 20th of September 2017, respectively. These two powerful Cat 5 hurricanes severely defoliated forest canopy and deposited massive amounts of litterfall in the forests across the island. We established a 1-ha research plot in each of four forests (Guánica State Forest, Río Abajo State Forest, Guayama Research Area and Luquillo Experiment Forest) before September 2016, and had collected one full year data of litterfall production prior to the arrival of Hurricanes Irma and Maria. Hurricane-induced litterfall was collected within one week after Hurricane Irma, and within two weeks after Hurricane Maria. Each litterfall sample was sorted into leaves, wood (branches and barks), reproductive organs (flowers, fruits and seeds) and miscellaneous materials (mostly dead animal bodies or feces) after oven-drying to constant weight. Annual litterfall production prior to the arrival of Hurricanes Irma and Maria varied from 4.68 to 25.41 Mg/ha/year among the four forests, and annual litterfall consisted of 50–81% leaffall, 16–44% woodfall and 3–6% fallen reproductive organs. Hurricane Irma severely defoliated the Luquillo Experimental Forest, but had little effect on the other three forests, whereas Hurricane Maria defoliated all four forests. Total hurricane-induced litterfall from Hurricanes Irma and Maria amounted to 95–171% of the annual litterfall production, with leaffall and woodfall from hurricanes amounting to 63–88% and 122–763% of their corresponding annual leaffall and woodfall, respectively. Hurricane-induced litterfall consisted of 30–45% leaves and 55–70% wood. Our data showed that Hurricanes Irma and Maria deposited a pulse of litter deposition equivalent to or more than the total annual litterfall input with at least a doubled fraction of woody materials. This pulse of hurricane-induced debris and elevated proportion

of woody component may trigger changes in biogeochemical processes and soil communities in these Puerto Rican forests.

Liu, X.; Zeng, X.; Zou, X. [and others]. 2018. Responses of Soil Labile Organic Carbon to a Simulated Hurricane Disturbance in a Tropical Wet Forest. Forests. 9(7): 420.
https://doi.org/10.3390/f9070420
Download: https://www.mdpi.com/1999-4907/9/7/420

Hurricanes are an important disturbance in the tropics that can alter forest ecosystem properties and processes. To understand the immediate influence of hurricane disturbance on carbon cycling, we examined soil labile organic carbon (LOC) in a Canopy Trimming Experiment (CTE) located in the Luquillo Experimental Forest of Puerto Rico. We trimmed tree canopy and deposited debris (CTDD) on the forest ground of the treatment plots in December 2014, and collected floor mass samples and 0–10 cm soil samples three weeks before the treatment, as well as at scheduled intervals for 120 weeks after the treatment. Within the first week following the CTDD treatment, the mean soil microbial biomass carbon (MBC) and soil LOC in the CTDD plots were significantly greater than in the control plots (soil MBC: 2.56 g/kg versus 1.98 g/kg, soil LOC: 9.16 g/kg versus 6.44 g/kg, respectively), and the mean turnover rates of soil LOC in the CTDD plots were significantly faster than in the control plots. The measured indices fluctuated temporally more in the CTDD plots than in the control plots, especially between the 12th and 84th week after the CTDD treatment. The treatment effect on soil LOC and its turnover rate gradually disappeared after the 84th week following the treatment, while higher levels of soil MBC in the CTDD plots than in the control plots remained high, even at the 120th week. Our data suggest that hurricane disturbance can accelerate the cycling of soil LOC on a short temporal scale of less than two years, but might have a longer lasting effect on soil MBC in a tropical wet forest.

Lodge, D.J.; Cantrell, S.A.; González, G. 2014. Effects of canopy opening and debris deposition on fungal connectivity, phosphorus movement between litter cohorts and mass loss. Forest Ecology and Management. 332: 11-21.
https://doi.org/10.1016/j.foreco.2014.03.002
Download: https://www.fs.usda.gov/treesearch/pubs/47197

Fungi are important for maintaining fast rates of decomposition in low quality tropical leaf litter via immobilization and translocation of limiting nutrients from sources to sinks and conserving nutrients after disturbance. Tropical trees often have low nutrient to carbon ratios. Disturbances such as hurricanes and logging transfer a large mass of green leaves with high nutrient concentrations to the forest floor, but the associated opening of the canopy dries the

litter, inhibiting basidiomycete fungi that play critical roles in lignin degradation and nutrient conservation. We conducted a replicated block factorial experiment designed to disentangle the individual and interactive effects of canopy opening and green debris deposition on phosphorus (P) content, mass loss and fungal connectivity in decomposing leaf cohorts in subtropical wet forest in the Luquillo Mountains of Puerto Rico. Though green leaves had higher P concentrations they did not decompose significantly faster than senesced leaves. Mass loss differed among treatments after 14, 40.5 and 53 weeks decomposition. Mass loss at 7 weeks was predicted by P concentration at 7 weeks; mass loss in senesced leaves at 14 weeks was predicted by abundance of fungal connections between the senesced litter cohort and forest floor at 7 weeks. Fungal connectivity and P accumulation at 7 weeks and mass loss of senesced leaves beginning at 14 weeks were significantly different from and lower in plots with trimmed canopy and no debris than in the untrimmed plots with debris. Litter moisture was previously found to be significantly lower under open than closed canopy, and we found that moisture was a significant predictor of fungal connectivity in both senesced and green leaves. Deposition of green leaves ameliorated the inhibitory effect of canopy opening on fungal connectivity between litter cohorts by retaining moisture; consequently fungal connectivity and mass loss in senescent leaves did not differ between the Trim + Debris and the control treatments. Phosphorus content of senesced leaves increased significantly by 7 weeks in both trimmed and untrimmed plots with added green debris and in the control plots. Based on mass balance calculations, both the underlying forest floor and overlying green leaves likely contributed P to the decomposing senesced leaf cohort. Fungal translocation of P through hyphal connections between litter cohorts explains some of the changes in P content. Though fungi were important in conserving P, most of the P that was likely leached from green leaves was not retained in the litter layer.

Lodge, D.J.; Scatena, F.N.; Asbury, C.E. [and other]. 1991. Fine Litterfall and Related Nutrient Inputs Resulting from Hurricane Hugo in Subtropical Wet and Lower Montane Rain Forests of Puerto-Rico. Biotropica 23(4): 336-342.
https://doi.org/10.2307/2388249
Download: https://www.fs.usda.gov/research/treesearch/66381

On 18 September 1989 Hurricane Hugo defoliated large forested areas of northeastern Puerto Rico. In two severely damaged subtropical wet forest sites, a mean of 1006-1083 g/m², or 419-451 times the mean daily input of fine litter (leaves, small wood, and miscellaneous debris) was deposited on the forest floor. An additional 928 g/m² of litter was suspended above the ground. A lower montane rain forest site received 682 times the mean daily fine litterfall. The concentrations of N and P in the hurricane leaf litter ranged from 1.1 to 1.5 and 1.7 to 3.3 times the concentrations of N and P in normal leaffall, respectively. In subtropical wet forest,

fine litterfall from the hurricane contained 1.3 and 1.5-2.4 times the mean annual litterfall inputs of N and P, respectively. These sudden high nutrient inputs apparently altered nutrient cycling.

Lodge, D.J.; Van Beusekom, A.E.; González, G. 2022. Disturbance reduces fungal white-rot litter mat cover in a wet subtropical forest. Ecosphere. 13: e3936. https://doi.org/10.1002/ecs2.3936
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3936

Fungi that bind leaf litter into mats and produce white-rot via degradation of lignin and other aromatic compounds influence forest nutrient cycling and soil fertility. Extent of white-rot litter mats formed by basidiomycete fungi in Puerto Rico decreased in response to disturbances-a simulated hurricane treatment executed by canopy trimming and debris addition in 2014, a drought in 2015, a treefall, and two hurricanes 10 days apart in September 2017. Percent fungal litter mat cover ranged from 0.4% after Hurricanes Irma and Maria to a high of 53% in forest with undisturbed canopy prior to the 2017 hurricanes, with means mostly between 10% and 45% of fungal litter mat cover in undisturbed forest. Drought decreased litter mat cover in both treatments, except in one control plot dominated by a drought-resistant fungus, *Marasmius crinis-equi*. Percent fungal litter mat cover sharply declined after hurricanes, a treefall, and a simulated hurricane treatment. Solar radiation was significantly inversely correlated with relative humidity (RH) and percent litter mat cover within each of the four climatic seasons. Solar radiation was also directly correlated with prior month litterfall, while RH was moderately correlated with throughfall, rain, and litter wetness. However, rainfall was inversely correlated with litter mat cover, possibly due to erosion or saturation during high rainfall events. Canopy opening reduced leaf fall and litter mat cover but these variables were not correlated except in winter. The main factor inhibiting basidiomycete fungi that bind leaf litter into mats was likely lower litter moisture associated with drought and increased solar radiation from canopy opening but secondary compounds in green litterfall may have contributed. Although higher litterfall likely increases fungal mat cover under closed canopy, changes in environmental factors apparently had a stronger inhibitory effect following canopy disturbances. Drought tolerance of some basidiomycete fungal litter mat species provided some resilience to drought.

Lodge, D.J.; Winter, D.; González, G. [and other]. 2016. Effects of Hurricane-Felled Tree Trunks on Soil Carbon, Nitrogen, Microbial Biomass, and Root Length in a Wet Tropical Forest. Forests. 7(11): 264. https://doi.org/10.3390/f7110264
Download: https://www.fs.usda.gov/treesearch/pubs/53184

Decaying coarse woody debris can affect the underlying soil either by augmenting nutrients that can be exploited by tree roots, or by diminishing nutrient availability through stimulation of microbial nutrient immobilization. We analyzed C, N, microbial biomass C and root length in closely paired soil samples taken under versus 20–50 cm away from large trunks of two species felled by Hugo (1989) and Georges (1998) three times during wet and dry seasons over the two years following the study conducted by Georges. Soil microbial biomass, % C and % N were significantly higher under than away from logs felled by both hurricanes (i.e., 1989 and 1998), at all sampling times and at both depths (0–10 and 10–20 cm). Frass from wood boring beetles may contribute to early effects. Root length was greater away from logs during the dry season, and under logs in the wet season. Root length was correlated with microbial biomass C, soil N and soil moisture (R = 0.36, 0.18, and 0.27, respectively; all p values < 0.05). Microbial biomass C varied significantly among seasons but differences between positions (under vs. away) were only suggestive. Microbial C was correlated with soil N (R = 0.35). Surface soil on the upslope side of the logs had significantly more N and microbial biomass, likely from accumulation of leaf litter above the logs on steep slopes. We conclude that decaying wood can provide ephemeral resources that are exploited by tree roots during some seasons.

Lomascolo, T.; Aide, T.M. 2001. Seed and seedling bank dynamics in secondary forests following Hurricane Georges in Puerto Rico. Caribbean Journal of Science. 37(3-4): 259-270.

This study describes the effect of Hurricane Georges (September, 1998) on the dynamics of seed and seedling banks in young secondary forests (25 yr) and mature secondary forests (60 yr) in abandoned pasture lands in Puerto Rico. In eight secondary forest sites, the seed bank was sampled in July 1998 and July 1999, and the seedling bank was sampled in November 1998 and November 1999. We collected data on number of species and individuals. In the seedling bank, mortality, recruitment and growth rate were estimated for one year. Hurricane damage was estimated for each site. The data suggest that sites in early stages of succession receive less damage from hurricane-force winds than older sites. As a consequence, after a hurricane later stages of succession present high light conditions, which result in high growth rate of pioneer and non-pioneer species. Although high light conditions may enhance seed germination from the seed bank, recruitment was low, and most post-hurricane regeneration came from pre-established individuals in the seedling bank. The recovery of secondary forests is usually studied in reference to time since abandonment, but this study shows that natural disturbances, particularly hurricanes, can affect the successional trajectory of secondary forests.

Lugo, A.E.; Frangi, J.L. 2003. Changes in Necromass and Nutrients on the Forest Floor of a Palm Floodplain Forest in the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science. 39(3): 265-272.
Download: https://www.fs.usda.gov/treesearch/pubs/30227

We studied changes that occurred between 1980 and 2000 in forest floor biomass (necromass + biomass of herbaceous plants), nutrient stocks, and plant composition ofa *Prestoea montana* floodplain forest. The forest was located in the Luquillo Mountains of Puerto Rico. Several storms and hurricanes passed near the study site during that period, the most severe being hurricane Hugo in 1989, and Georges in 1998. Hugo opened the canopy and increased the nutrient and biomass stocks of the forest floor. Six years after the passage of Hugo and two years after Georges, the forest floor necromass was at pre-hurricane (1980) levels. By October 2000, fine litter mass and nutrient stocks were below 1980 and 1990 levels (respectively). However, the distribution of biomass and nutrients on the forest floor in 2000 was different from pre-Hugo conditions due to the growth of herbaceous vegetation that included grasses and ferns that were not present in 1980. These plants concentrated nutrients in disproportion to their biomass and had leaves with low C/N. Attention to change in species composition on the forest floor as well as to necromass and nutrient distribution in fine litter, improves understanding of the recovery of the forest floor from disturbance.

Lugo, A.E.; Frangi, J.L. 2016. Long-Term Response of Caribbean Palm Forests to Hurricanes. Caribbean Naturalist. 1: 157-175.
Download: https://www.fs.usda.gov/treesearch/pubs/52762

We studied the response of *Prestoea montana* (Sierra Palm, hereafter Palm) brakes and a Palm floodplain forest to hurricanes in the Luquillo Experimental Forest in Puerto Rico. Over a span of 78 years, 3 hurricanes passed over the study sites for which we have 64 years of measurements for Palm brakes and 20 years for the Palm floodplain forest. For each stand, species composition, species density, basal area, tree density, rates of tree ingrowth and mortality, and importance value of tree species were assessed. We also estimated stand and Palm population aboveground biomass for the Palm floodplain forest. We found that different forest attributes such as basal area and tree density exhibited different temporal response patterns to hurricanes. The passing of 2 hurricanes in less than 10 years shifted the forest-response pattern of Palm brakes into a different trajectory with wider oscillations than before the 1989 hurricane. Neither Palm forest type reached steady state during the period of observation. Palm brakes spent about 50 of 64 years of the study in a transition state, and during the last 14 of those years, *Cecropia schreberiana* (Yagrumo) displaced the Palms as the species with the highest importance value, likely due to hurricane effects. The Palm floodplain forest remained in a transition mode over the 20-year span of the study. The results of the

study showed that stands located on the leeward of hurricanes experienced less structural and species-composition changes and had more time to recover from hurricane effects than those exposed to the windward path of the hurricane. Caribbean Palm forests are dynamic systems whose structure, species composition, species density, and processes are finely coupled to frequency and intensity of hurricanes. Because Palm forest dynamics are closely tied to hurricanes, it is possible to anticipate that any future change in the frequency or intensity of hurricanes is likely to influence these forest attributes, including species ranking by importance value.

Lugo, A.E.; Rodríguez Pedraza, C.D.; Fremont, I. [and other]. 2017. Response to Hurricanes of *Pinus caribaea var hondurensis* Plantations in Puerto Rico. Caribbean Naturalist. 43:1-16.
Download: https://www.fs.usda.gov/treesearch/pubs/56568

We studied the response to hurricanes of 2 *Pinus caribaea Morelet var. hondurensis Barr*. & Golf. (Honduran Pine) plantations and paired secondary forests over a period of 32 years (1982 to 2014). Plantations differed in age (38 and 53.5 years old), as did the paired secondary forests. The study included the passage of 2 hurricanes (1989 and 1998). The hurricanes altered forest structure by lowering the basal area and tree density, accelerated tree mortality to over 5% per year and ingrowth rate to over 200 stems/ha at the Cubuy plantation, caused variability and reduction in individual tree growth rates, and dramatically changed species composition and dominance of stands. Honduran Pines were heavily affected by the hurricanes, losing dominance, and almost disappearing from the Cubuy site, in effect converting that pine plantation into a secondary forest with few pines. The susceptibility of Honduran Pine to strong winds raises concern about its suitability for plantation forestry in the hurricane belt of the Caribbean. Their use for commercial timber production would have to consider the recurrence of hurricanes in the region.

Mariani-Ríos, A.; Maldonado-Benítez, N.; Ramírez, A. 2022. Natural history of Odonata assemblages in tropical streams in Puerto Rico. Neotropical Biodiversity. 8: 112-123. https://doi.org/10.1080/23766808.2022.2043699
Download: https://www.tandfonline.com/doi/epdf/10.1080/23766808.2022.2043699?needAccess=true&role=button

Freshwater macroinvertebrates play an important role in maintaining stream food webs. Odonata (dragonflies and damselflies) are important top predators in these communities and serve as indicators of stream health. Our understanding of odonate assemblages is limited in the Caribbean and the natural history of most odonate species in the region remains unknown. The focus of this research is to study the natural history of odonate species in

headwater montane streams following major hurricane impacts in Puerto Rico. We monitored assemblages from August 2018 to July 2019 in two headwater streams within El Yunque National Forest, Puerto Rico. The study streams drain a protected forest, with aseasonal precipitation patterns, relatively constant water temperature, and flashy hydrographs that quickly respond to rain events. We sampled 226 adults and 550 larvae, dominated by three Caribbean endemics: *Scapanea frontalis*, *Macrothemis celeno*, and *Telebasis vulnerata*. Only *S. frontalis* and *M. celeno* were abundant enough to assess the temporal patterns and their natural history. Larval density fluctuated throughout the year with short peaks in abundance during different times of the year, according to the species. Small individuals (<= 10 mm body length) were more abundant than the large ones. However, all size classes were present during the year. The dominant species, *S. frontalis* and *M. celeno*, had continuous development patterns, without identifiable size classes and multiple overlapping generations. The exception was the last stadium that formed a separate group in the body length vs head width plots. Species had clear habitat preferences; *S. frontalis* was abundant in riffles and preferred areas with high amounts of cobble. *Macrothemis* celeno prefers pool habitats with fine substrates. While we found trends for negative relations between abundance and discharge, canopy cover, water temperature, and rainfall, none was statistically significant. Observed patterns suggest a lack of strong temporal seasonality in the natural history of Odonata, which coincides with the aseasonal environment of streams draining our study area. Overall, our study is the first to assess temporal variability of Odonata assemblages in montane streams of Puerto Rico and provides information on Caribbean endemic species.

McDowell, W.H.; Brereton, R.L.; Scatena, F.N. [and others]. 2013. Interactions between lithology and biology drive the long-term response of stream chemistry to major hurricanes in a tropical landscape. Biogeochemistry. 116: 175-186.
https://doi.org/10.1007/s10533-013-9916-3
Download: https://www.fs.usda.gov/treesearch/pubs/46664

Humid tropical forests play a dominant role in many global biogeochemical cycles, yet long-term records of tropical stream chemistry and its response to disturbance events such as severe storms and droughts are rare. Here we document the long-term variability in chemistry of two streams in the Luquillo Mountains, Puerto Rico over a period of 27 years. Our two focal study watersheds, the Río Icacos and Quebrada Sonadora, both drain several hundred hectares of tropical wet forests, and each received direct hits from Hurricanes Hugo (1989) and Georges (1998). They differ primarily in lithology (granitic vs. volcaniclastic) and elevation. Changes in major cations, anions, silica, and dissolved organic carbon were minimal over the study period, but the concentrations of nitrate show a strong response to hurricane disturbance and the longest time to recovery. Potassium also showed a large, although less consistent,

response to disturbance. In the granitic terrain, nitrate concentrations exceeded long-term pre-hurricane background levels for over a decade, but were elevated in the volcaniclastic terrain for only 1–2 years. Lithology appears to be the primary driver explaining the different response trajectories of the two watersheds. In the granitic terrain, which showed slow recovery to pre-hurricane conditions, the quartz diorite bedrock weathers to produce coarser soils, deeper groundwater flow paths, and riparian zones with sharp spatial variation in redox conditions and very high nitrogen levels immediately adjacent to the stream. Groundwater flow paths are shallow and the levels of N in streamside groundwater are much lower in the volcaniclastic terrain. The recovery of vegetation following hurricane disturbance appears similar in the two watersheds, suggesting that the extent of structural damage to canopy trees determines the magnitude of NO3 increases, but that the duration of elevated concentrations in stream water is a function of lithology.

McDowell, W.H.; Liptzin, D. 2014. Linking soils and streams: Response of soil solution chemistry to simulated hurricane disturbance mirrors s tream chemistry following a severe hurricane. Forest Ecology and Management. 332: 56-63.
https://www.sciencedirect.com/science/article/pii/S0378112714003624?via%3Dihub
Download: https://www.fs.usda.gov/research/treesearch/48372

Understanding the drivers of forest ecosystem response to major disturbance events is an important topic in forest ecology and ecosystem management. Because of the multiple elements included in most major disturbances such as hurricanes, fires, or landslides, it is often difficult to ascribe a specific driver to the observed response. This is particularly true for the long-term effects of hurricanes on forest ecosystem nutrient cycling. Hurricane disturbance opens the forest canopy by removing leaves and branches or snapping boles, and in so doing turns living biomass into debris that is deposited on the forest floor. At the watershed scale, past work in the Luquillo Mountains of Puerto Rico shows that these changes in forest structure and detrital dynamics result in large increases in stream water nitrate and potassium concentrations in streams draining volcaniclastic terrain. The Canopy Trimming Experiment (CTE) was designed to simulate the major effects of hurricane disturbance, and disentangle the effects of canopy opening and debris addition on forest biology and biogeochemistry following a hurricane. Using the chemistry of soil solution as an integrated indicator of biogeochemical response to hurricane simulation, the experimental manipulations show that the synergistic effects of both canopy opening and debris addition are needed to elicit one of the whole-watershed responses to hurricanes, a large pulse of nitrate (NO^3) concentration in stream water that lasted approximately 18 months. Manipulation of either canopy openness or debris addition alone had little effect on soil solution chemistry for NO^3, or for any other solute measured (dissolved organic matter,

phosphate, ammonium, major cations and anions, and silica). None of the treatments resulted in the increased potassium (K) seen in stream water following hurricane disturbance. For NO^3, the time course of response and recovery following combined treatments of canopy opening and debris addition was similar to that observed in stream water after actual hurricanes. The CTE provided further evidence that tree regrowth following hurricane disturbance controls the return of NO^3 concentrations to pre-hurricane levels in this tropical forest. The lack of response in K to hurricane simulation suggests that leaching of the added debris, which was not captured in the experimental manipulations, is a major driver of K concentrations following disturbance. Hurricane disturbance, which is significant in many humid tropical forests, results in pulsed outputs of nitrogen in stream water that can be clearly ascribed to interactions between damage and recovery of canopy vegetation, and decomposition of detrital inputs on the forest floor.

McDowell, W.H.; Potter, J.D. 2022. Context dependence in a tropical forest: Repeated disturbance reduces soil nitrate response but increases phosphate. Ecosphere. 13: e4068. https://doi.org/10.1002/ecs2.4068
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.4068

Hurricanes and other extreme events are increasing in many regions, yet their long-term impacts on ecosystem function are uncertain. In forested ecosystems, soil solution chemistry provides an important tool to assess the impacts of disturbance on nutrient cycling and dissolved organic carbon dynamics. Here, we address the dependence of soil solution chemistry on disturbance regime using a novel combination of both experimental and observational results collected over a period of 16 years in montane tropical sites in the Luquillo Experimental Forest of Puerto Rico. Soil solution was sampled following various combinations of canopy trimming and detrital manipulation (2004), repeated manipulation (2014),drought (2015), and Hurricane Maria (2017). Soil solution was sensitive to disturbance but resilient, with return to baseline after 12-18 months. Any disturbance regime that involved loss of canopy and detrital inputs to the forest floor resulted in increased nitrate concentrations, but the response declined with repeated disturbance. Lysimeters in plots that had received no experimental manipulation had 1.5 times higher response to Hurricane Maria than those previously manipulated. The response to disturbance thus showed clear context dependence, with disturbance history affecting disturbance response. Among the nutrients and major ions, only nitrate showed a response to experimental manipulations, drought, and Hurricane María. In contrast to nitrate, soil solution potassium was unaltered by initial experimental manipulation but increased dramatically following drought and Hurricane Maria. Phosphorus only increased following Hurricane Maria and only in plots that had twice received experimental trimming and deposition of cut branches on the forest

floor. Stoichiometry of dissolved organic matter also changed in these plots, with decreased carbon to nitrogen ratios. The potassium response suggests that damage to roots from tropical cyclones and drought is an important driver of the biogeochemical response to tropical storms. Dampening of soil nitrogen losses and increases in phosphorus losses following successive disturbance events indicates that increased frequency of tropical storms and droughts will result in fundamental alteration of soil biogeochemical cycles, with uncertain effects on forest structure.

McDowell, W.H.; McSwiney, C.P.; Bowden, W.B. 1996. Effects of Hurricane Disturbance on Groundwater Chemistry and Riparian Function in a Tropical Rain Forest. Biotropica. 28(4a): 577-584. https://doi.org/10.2307/2389098

The long-term response of shallow groundwater chemistry to the canopy disturbance and defoliation associated with Hurricane Hugo was studied at two sites in the Luquillo Experimental Forest, Puerto Rico. The sites differed in bedrock type, dominant vegetation, and availability of pre-hurricane data. At the primary study site, the Bisley catchment, hurricane disturbance resulted in increased concentrations of NO_3-, NH_4+, dissolved organic N, base cations, Cl-, and SiO_2 in groundwater within 5 mo of the hurricane. The largest relative change in concentration occurred for K+, which increased from 0.7 to as high as 13 mg/L, concentrations were still 1.3 mg/L 5.5 yr after the hurricane. Most other solutes had returned to background levels within 1-2 yr of the hurricane. At the secondary study site, the Icacos catchment, NO_3- concentrations peaked at 1.1 mg/L one yr after the hurricane and decreased to nearly zero 5.5 yr after the hurricane. At both sites, NO_3- concentrations were higher in upslope wells than in those closer to the stream. Overall, riparian processes appear to reduce but not eliminate hydrologic losses of N following catastrophic disturbance. The nature of the long-term biogeochemical response to disturbance in this tropical rain forest ecosystem is similar to that observed in some montane temperate forests, and the time course of recovery appears to be associated with the speed with which vegetation regrows following disturbance.

McMahan, E.A.; Blanton, C.M. 1993. Effects of Hurricane Hugo on a Population of the termite *Nasutitermes costalis* in the Luquillo Experimental Forest, Puerto Rico. Caribbean Journal of Science. 29(3-4): 202-208.

Within a month after Hurricane Hugo's September 1989 passage over Puerto Rico's Luquillo Experimental Forest, surveys were initiated on a *Nasutitermes costalis* population to document the number and sizes of nests and above-ground gallery construction. When the population was reexamined in 1991, no significant change in number of nests or in gallery construction was observed, which suggested neither long term deleterious effects from the storm's erosive

forces nor advantageous effects from the increase of food (dead wood). However, at the two-year post-Hugo interval, average increase in nest height was significantly greater than in a similar two-year study of *N. costalis* in the same area in 1967-1969. This difference in growth rate can be explained in terms of initial nest size. The immediately-post-Hugo nests of 1989 were considerably smaller than the nests measured in 1967, a result perhaps of the hurricane's erosive effects. Their temporary growth advantage may be attributable to a higher ratio of inhabitants to nest volume within the 1989 nests (because of the storm's forcible concentration of the termites into the lower, safer reaches). In addition, smaller nests have a more favorable surface-volume relationship for gaseous exchange, enhancing conditions for nest repair and/or population increase within the colony.

Meléndez-Ackerman, E.; Calisto-Pérez, C.; Morales-Vargas, M. [and other]. 2003. Post-hurricane recovery of a herbaceous understorey plant in a tropical rain forest in Puerto Rico. Journal of Tropical Ecology. 19(6): 677-684. https://doi.org/10.1017/S0266467403006072

Ecologists agree on the importance of hurricanes in community dynamics in tropical forests but little is known of the responses of herbaceous species to large disturbances. The passage of Hurricane Georges over the island of Puerto Rico provided a unique opportunity to study the post-hurricane recovery of *Heliconia caribaea*, a large understorey herb. Five weeks after Georges, the types of vegetative damage, mortality and recovery were recorded and their relationship with plant size was established. The relationship between recovery strategy and leaf or stem damage severity was also determined. The abundance of *H. caribaea* seedlings in sites with severe or little forest canopy damage was recorded to determine the effects of canopy cover on seedling establishment. Most individuals showed severe leaf and stem damage. This was not related to plant size. Mortality was low and caused by fallen trees. Recovery was not associated with severity of leaf damage but more individuals with no signs of regeneration appeared among plants that had severe stem damage. Seedling abundance was higher in areas with severe canopy damage relative to those with closed canopy suggesting that hurricanes may benefit *H. caribaea* by creating suitable habitats for seedling establishment. We argue that recovery strategies like those exhibited by *H. caribaea* may be common among understorey plants, particularly in areas regularly subjected to large-scale disturbances.

Moreno, I.U.; Barberena-Arias, M.F.; González, G. 2022. Canopy opening increases leaf-shredding arthropods and nutrient mineralization but not mass loss in wet tropical forest. Ecosphere. 13: e4084. https://doi.org/10.1002/ecs2.4084
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.4084

Hurricanes alter forest habitat by opening the canopy and depositing fresh wood and leaves. The objectives of this study were to evaluate the effects of hurricane and drought-driven changes to forests on green litter decomposition, invertebrate communities, and nutrient mineralization over a short period (6 months) after disturbance. We used three complete replicated blocks with two canopy treatments: control and trim + detritus. Green leaves were enclosed in litterbags of three different mesh sizes to determine the effect of soil fauna of varying body sizes. Litterbags were retrieved from the field after 21, 35, 84, and 168 days and transported to the laboratory in individually sealed plastic bags. We extracted and identified invertebrates, measured leached and mineralized litter nutrients using ion resin membranes placed for 1 week under the leaves inside the litterbags, and determined litter mass loss. Additional resin membranes were placed in the lowest litter layer above the mineral soil. The number of arthropod taxonomic groups and nutrient mineralization differed significantly between control and trim + detritus. Regardless of mesh size, bags in control plots had consistentlyhigher invertebrate richness than in trim + detritus plots. Nitrogen mineralization and phosphorous mineralization were significantly higher in trim + detritus in large mesh size, and decomposer arthropod abundance was highest in large-sized mesh bags. These data suggest that within functional categories, variations in feeding behavior among arthropod ordersmay affect the release of nutrients from organic matter. Percent mass loss did not differ between canopy treatments orlitterbag mesh sizes, but instead decreased during drought. Invertebrate composition, but not abundance, differed significantly between canopy treatments with greater dominance by shredders (Lepidoptera and Diptera larvae) in trim +detritus, which corresponded to higher rates of nutrient mineralization from green leaves. These results suggest that regional drought dominated the mesoclimate surpassing any microclimate variation in response to canopy treatments. Sincemass loss did not differ between canopy treatments or litterbag mesh sizes, our results suggest that differences in short-term nutrient fluxes from green litter are mostly related to changes in the litter invertebrate food web rather than rates of decomposition.

O'Brien, S.T.; Hayden, B.P.; Shugart, H.H. 1992. Global climatic change, hurricanes, and a tropical forest. Climatic Change. 22: 175-190. https://doi.org/10.1007/BF00143026

Most, if not all forests in the Caribbean are subject to occasional disturbances from hurricanes. If current general circulation model (GCM) predictions are correct, with doubled atmospheric CO_2 ($2 \times CO_2$), the tropical Atlantic will be between 1 °C and 4 °C warmer than it is today. With such a warming, more than twice as many hurricanes per year could be expected in the Caribbean. Furthermore, Emanuael (1987) indicates that in a warmed world the destructive potential of Atlantic hurricanes could be increased by 40% to 60%. While speculative, these increases would dramatically change the disturbance regimes affecting

tropical forests in the region and might alter forest structure and composition. Global warming impacts through increased hurricane damage on Caribbean forests are presented. An individual tree, gap dynamics forest ecosystem model was used to simulate the range of possible hurricane disturbance regimes which could affect the Luquillo Experimental Forest in Puerto Rico. Model storm frequency ranged from no storms at all up to one storm per year; model storm intensity varied from no damage up to 100% mortality of trees. The model does not consider the effects of changing temperature and rainfall patterns on the forest. Simulation results indicate that with the different hurricane regimes a range of forest types are possible, ranging from mature forest with large trees, to an area in which forest trees are never allowed to reach maturity.

Ostertag, R.; Scatena, F.N.; Silver, W.L. 2003. Forest Floor Decomposition Following Hurricane Litter Inputs in Several Puerto Rican Forests. Ecosystems. 6(3): 261-273.
https://doi.org/10.1007/PL00021512
Download: https://www.fs.usda.gov/treesearch/pubs/30175

Hurricanes affect ecosystem processes by altering resource availability and heterogeneity, but the spatial and temporal signatures of these events on biomass and nutrient cycling processes are not well understood. We examined mass and nutrient inputs of hurricane-derived litter in six tropical forests spanning three life zones in northeastern Puerto Rico after the passage of Hurricane Georges. We then followed the decomposition of forest floor mass and nutrient dynamics over 1 year in the three forests that experienced the greatest litter inputs (moist, tabonuco, and palm forests) to assess the length of time for which litter inputs influence regeneration and nutrient cycling processes. The 36-h disturbance event had litterfall rates that ranged from 0.55 to 0.93 times annual rates among the six forests; forest floor ranged between 1.2 and 2.5 times pre-hurricane standing stocks. The upper elevation forest sites had the lowest non-hurricane litterfall rates and experienced the lowest hurricane litterfall and the smallest relative increase in forest floor standing stocks. In the three intensively studied forests, the forest floor returned to pre-hurricane values very quickly, within 2–10 months. The palm forest had the slowest rate of decay ($k = 0.74 \pm 0.16\ y^{-1}$), whereas the tabonuco forest and the moist forest had similar decay rates (1.04 ± 0.12 and 1.09 ± 0.14, respectively). In the moist forest, there were short-term increases in the concentrations of nitrogen (N), phosphorus (P), calcium (Ca), and magnesium (Mg) in litter, but in the other two forests nutrient concentrations generally decreased. The rapid disappearance of the hurricane inputs suggests that such pulses are quickly incorporated into nutrient cycles and may be one reason for the extraordinary resilience of these forests to wind disturbances.

Ostertag, R.; Silver, W.L.; Lugo, A.E. 2005. Factors Affecting Mortality and Resistance to Damage Following Hurricanes in a Rehabilitated Subtropical Moist Forest. Biotropica. 37(1): 16-24. https://doi.org/10.1111/j.1744-7429.2005.04052.x
Download: https://www.fs.usda.gov/research/treesearch/66367

The ability to resist hurricane damage is a property of both individuals and communities, and can have strong effects on the structure and function of many tropical forests. We examined the relative importance of tree size, species, biogeographic origin, local topography, and damage from previous storms in long-term permanent plots in a rehabilitated subtropical moist forest in Puerto Rico following Hurricane Georges in order to better predict patterns of resistance. Severe damage included uprooted trees, snapped stems, or crowns with greater than 50 percent branch loss. Hurricane induced mortality after 21 mo was 5.2 percent/yr, more than seven times higher than background mortality levels during the nonhurricane periods. Species differed greatly in their mortality and damage patterns, but there was no relationship between damage and wood density or biogeographic origin. Rather, damage for a given species was correlated with mean annual increment, with faster growing species experiencing greater damage, suggesting that growth rate may reflect a variety of life history tradeoffs. Size was also predictive of damage, with larger trees suffering more damage. Trees on ridges and in valleys received greater damage than trees on slopes. A strong relationship was noted between previous hurricane damage and present structural damage, which could not solely be explained by the patterns with size and species. We suggest that resistance of trees to hurricane damage is therefore not only correlated with individual and species characteristics but also with past disturbance history, which suggests that in interpreting the effects of hurricanes on forest structure, individual storms cannot be treated as discrete, independent events.

Pandey, M.; Schowalter, T.M. 2022. Canopy arthropod responses to repeated canopy opening in a wet tropical forest. Ecosphere. 13: e4177.
https://doi.org/10.1002/ecs2.4177
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.4177

With predictions of increased frequency of intense hurricanes, it is increasingly crucial to understand how biotic and abiotic components of forests will be affected. This study describes canopy arthropod responses to repeated experimental and natural canopy opening at the Luquillo Experimental Forest Long-term Ecological Research Site (LTER) in Puerto Rico. The canopy trimming experiment (CTE1) treatments were started in 2004, and a second trimming (CTE2) was conducted in 2014, to study effects of increased hurricane frequency at the site. Paired disturbed plots with canopy trimmed (trim) and undisturbed plots with no trimming (no trim) were replicated in three experimental blocks. Arthropods were sampled by bagging

branches on seven representative early and late successional overstory and understory tree species annually from 2004 to 2009 for CTE1 and 2015 to 2019 for CTE2. In addition to the experimental manipulation, the CTE site was disturbed by Hurricane Maria (Category 4) in September 2017, providing an additional natural canopy opening to the experiment. We evaluated the effect of the second experimental trimming, compared canopy arthropod responses to the three canopy-opening events, and compared the effects of experimental trimming and natural canopy opening by Hurricane Maria. The second experimental canopy trimming produced canopy arthropod responses consistent with hurricane disturbances, with sap-sucking herbivores increasing in abundance on the trimmed plots, whereas other functional groups generally declined in abundance in disturbed plots. Responses to the first and second trimmings were generally similar. However, Hurricane Maria exacerbated the responses, indicating the likely effect of increased hurricane frequency and intensity.

Parrotta, J.A.; Lodge, D.J. 1991. Fine Root Dynamics in a Subtropical Wet Forest Following Hurricane Disturbance in Puerto Rico. Biotropica. 23(4a): 343-347. https://doi.org/10.2307/2388250
Download: https://www.fs.usda.gov/research/treesearch/66368

Fine root dynamics were evaluated at four sites in a subtropical wet forest in Puerto Rico over a period of 13 months following disturbance by Hurricane Hugo in September 1989 Live fine root standing stocks (to a depth of 10 cm) declined to zero over a three-month period after the hurricane and fluctuated greatly thereafter. Maximum fine root biomass (49 g/m^3) occurred in June 1990. Dead root standing stocks (mean 423 g/m^3) were relatively constant through the study period. Recovery of fine roots following the initial hurricane-related mortality appears to be a slow process, regulated at least initially by environmental factors such as precipitation.

Pascarella, J.B.; Aide, T.M. Zimmerman, J.K. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. Forest Ecology and Management. 199(2-3): 379-393. https://doi.org/10.1016/j.foreco.2004.05.041

We examined the short-term (4–5 years) dynamics of stand structure and species composition of two chronosequences of secondary forest stands derived from abandoned cattle pastures (15–81 years since abandonment) in the Luquillo and Carite Mountains of eastern Puerto Rico. In 1998, Hurricane Georges struck Puerto Rico, affecting both chronosequences. Stem densities decreased in all sites with a significant effect of age-class. Intermediate-aged sites had the greatest decrease in density and the largest change in the distribution of size classes. Although there was a significant decrease in the small size classes (<10 cm dbh), due to physical damage from falling debris, there was a large increase in the 10–20 cm dbh classes,

due to growth of surviving stems. Basal area decreased in 11 of the 15 sites and showed only a slight gain in the other sites. Species richness decreased in all but one site and there was a greater proportional loss of shrub species than tree species. Multivariate ordination successfully placed the resampled sites within their original ordinations with acceptable stress, indicating there was no significant change in species composition or deviation from successional pathways during the period. Compared with effects of land-use, hurricanes create minor variation from expected successional pathways. However, hurricanes contribute to regional- and landscape-scale variation in both stand structure and species composition.

Prates, M.O.; Dey, D.K.; Willig, M.R. [and other]. 2010. Intervention Analysis of Hurricane Effects on Snail Abundance in a Tropical Forest Using Long-Term Spatiotemporal Data. Journal of Agricultural, Biological, and Environmental Statistics. 16(1): 142-156. https://doi.org/10.1007/s13253-010-0039-1

Large-scale natural disturbances, such as hurricanes, have profound effects on populations, either directly by causing mortality, or indirectly by altering ecological conditions or the quantity, quality, and spatial distribution of resources. In the last 20 years, two major disturbances, Hurricane Hugo in 1989 and Hurricane Georges in 1998, struck the Luquillo Mountains of Puerto Rico, providing an unique opportunity to understand the long-term effects of recurrent disturbances on the abundance of species. *Nenia tridens* is one of the most abundant and pervasive terrestrial gastropods in the Luquillo Mountains. Estimates of yearly abundance of *N. tridens* from 40 sites on the Luquillo Forest Dynamics Plot from 1991 to 2007 facilitate the development of a spatiotemporal model with intervention effects on the mean abundance over time in response to each hurricane. Intervention effects characteristically decay over time, similar to those in a time series analysis. Model parameters were estimated in a Bayesian framework. Model comparison and diagnostics suggest that our intervention model provides a plausible description of hurricanes effects on the abundances of *N. tridens* and may be useful for studying long-term spatiotemporal dynamics from the perspective of disturbance and succession.

Prather, C. 2014. Divergent responses of leaf herbivory to simulated hurricane effects in a rainforest understory. Forest Ecology and Management. 332: 87-92. https://doi.org/10.1016/j.foreco.2014.06.040
Download: https://www.fs.usda.gov/treesearch/pubs/48302

Hurricanes are major disturbances in many forests, but studies showing effects of natural hurricanes on herbivory rates have yielded mixed results. Forest managers could benefit from a better understanding of the effects of disturbances on herbivory to manage for particular

recovery or restoration goals after anthropogenic or natural disturbances, such as logging and windstorms. I measured herbivory on eight understory plant species that are common pioneer and non-pioneer species in a rainforest in Puerto Rico, following experimental manipulation of forest plots to simulate the two major effects of a hurricane (canopy opening and a detrital pulse). I expected that greater leaf production and leaf quality would result from canopy trimming and detritus (debris) addition to the forest floor, respectively, and that both treatments would enhance herbivory rates independently and especially in combination. I found a significant interaction of trim and debris treatments that affected plant species within pioneer and non-pioneer plant groups differently: a debris pulse or canopy trimming alone stimulated understory herbivory over time on non-pioneer and pioneer plants, respectively, but the combination of these two treatments had no effect on herbivory rates. Specifically, herbivory was higher on pioneer plants in plots where the canopy was trimmed but debris had not been added, whereas herbivory was higher on non-pioneer plants in plots where debris was added to the forest floor under intact canopy conditions. Therefore, different mechanisms apparently controlled herbivory of pioneer and non-pioneer species. Pioneer plants likely experienced enhanced herbivory in trimmed plots in part because of the increased densities of pioneer plants responding to canopy trimming; pioneer plants were temporarily less abundant in debris addition plots. Non-pioneer species may have experienced greater herbivory in debris addition plots in part because of increased foliar quality resulting from enhanced nutrient availability associated with the debris pulse. Future, complementary greenhouse and field mesocosm experiments that manipulate the factors likely contributing to these results would help to reconcile results from previous studies that have documented both increases and decreases in herbivory or certain herbivore taxonomic groups resulting from natural hurricanes. Understanding the mechanisms that affect herbivory after hurricanes is important because herbivory can affect nutrient cycling, plant community structure, and ultimately forest recovery after disturbance.

Presley, S.J.; Willig, M.R. 2023. Long-term responses to large-scale disturbances: spatiotemporal variation in gastropod populations and communities. Oikos. 7: e09605. https://doi.org/10.1111/oik.09605

The Anthropocene is characterized by complex, primarily human-generated, disturbance regimes that include combinations of long-term press (e.g. climate change, pollution) and episodic pulse (e.g. cyclonic storms, floods, wildfires, land use change) disturbances. Within any regime, disturbances occur at multiple spatial and temporal scales, creating complex and varied interactions that influence spatiotemporal dynamics in the abundance, distribution and biodiversity of organisms. Moreover, responses to disturbance are context dependent, with the legacies of previous disturbances affecting responses to ensuing perturbations. We use

three decades of annual data to evaluate the effects of repeated pulse disturbances and global warming on gastropod populations and communities in Puerto Rico at multiple spatial scales. More specifically, we quantify 1) the relative importance of large-scale and small-scale aspects of disturbance on variation in abundance, biodiversity and species composition; and 2) the spatial scales at which populations and communities integrate information in the spatially heterogenous environments created by disturbances. Gastropods do not exhibit consistent decreases in abundance or biodiversity in association with global warming: abundance for many species has increased over time and species richness does not evince a temporal trend. Nonetheless, gastropods are sensitive to hurricane severity, spatial environmental variation and successional trajectories of the flora. In addition, they exhibit context dependent (i.e. legacy effects) responses that are scale dependent. The Puerto Rican biota has evolved in a disturbance-mediated system. This historical exposure to repeated, severe hurricane-induced disturbances has imbued the biota with high resistance and resilience to the current disturbance regime, resulting in an ability to persist or thrive under current environmental conditions. Nonetheless, these ecosystems may yet be threatened by worsening direct and indirect effects of climate change. In particular, more frequent and severe hurricanes may prevent the establishment of closed canopy forests, negatively impacting populations and communities that rely on these habitats.

Presley, S.J.; Willig, M.R. 2022. Long-term responses of gastropods to simulated hurricanes in a tropical montane rainforest. Ecosphere. 13: e3928.
https://doi.org/10.1002/ecs2.3928
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3928

Climate-induced disturbances such as hurricanes affect the structure and functioning of ecosystems, especially those in the Caribbean Basin, where high-energy storms have long affected ecosystem dynamics. Because climate change will likely continue to alter the frequency and intensity of hurricanes in the Caribbean, it is increasingly important to understand the mechanistic bases for ecosystem responses. Although long-term surveys and nonmanipulative "natural experiments" provide considerable insight, manipulative experiments are required to decouple confounded factors associated with high-intensity storms. To address this, we exploited a replicated factorial design to experimentally isolate the long-term effects of canopy opening and debris deposition on population- and community-level characteristics of gastropods in the Luquillo Experimental Forest of Puerto Rico. The canopy trimming experiment included four treatments:(1) the reference treatment received no manipulations; (2) canopy trimmed, but debris from trimming not deposited on the forest floor (trim only); (3) canopy not trimmed, but debris deposited on the forest floor (debris only); and (4) canopy trimmed and debris deposited on the forest floor (trim and debris).

After 10 years, the trim and debris treatment was repeated to simulate reoccurring hurricane events, whereas the trim-only and debris-only treatments were not subject to additional manipulation at this time. We evaluated responses to treatment and time for gastropod populations (abundance)and communities (biodiversity and composition). Population-level responses were species specific. Three species and total gastropod abundance exhibited consistent responses to treatments regardless of time, four species exhibited consistent temporal trends regardless of treatment, and five species exhibited an interaction in which the effects of time depended on treatment. In general, point-, alpha-, and gamma-biodiversity decreased through time, whereas beta-biodiversity increased through time. Gastropod populations and communities were resistant and resilient to the simulated disturbances, exhibiting quick recovery from any short-term changes in abundance or biodiversity. From an evolutionary perspective, long-term exposure to hurricane-induced disturbances likely leads to species-specific adaptations that enhance resistance and resilience.

Quebbeman, A.W.; Menge, D.N.L.; Arellano, G. [and others]. 2022. A Severe Hurricane Increases Carbon Dioxide and Methane Fluxes and Triples Nitrous Oxide Emissions in a Tropical Forest. Ecosystems. 25(8): 1754-1766.
https://doi.org/10.1007/s10021-022-00794-1

Tropical cyclones (for example, hurricanes, typhoons) are expected to intensify under a warming climate, with uncertain effects on tropical forests. These ecosystems contribute disproportionately to greenhouse gas (GHG; carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O)) fluxes globally but there is high uncertainty in how these fluxes will respond to the projected increase in the frequency of severe tropical cyclones. To examine how these natural disturbance events may alter ecosystem processes in tropical forests, we studied the effects of Hurricane Maria (2017), a category 4 storm, on soil GHG fluxes from a forest in Puerto Rico. We also asked how environmental conditions, namely severity of tree canopy damage and topographic position, influenced spatial heterogeneity in post-hurricane soil GHG emissions. Seven months after Hurricane Maria, we observed an 18% increase in soil CO_2 fluxes, a switch in CH_4 fluxes from net consumption toward net production, and a threefold increase in N_2O emissions relative to pre-hurricane fluxes. None of these fluxes were sensitive to topographic heterogeneity or the magnitude of tree canopy damage, in contrast to the marked soil GHG flux sensitivity to topography prior to the storm. Upscaling the increase in soil N_2O emissions to the ecosystem level shows that greater emissions of soil N_2O following hurricanes also led to high rates of nitrogen loss that, if sustained over a year, would be equivalent to 30% of estimated losses of inorganic nitrogen to runoff and groundwater. Additionally, the combined hurricane-induced increases in soil GHGs suggest a 25% increase in the contribution of soil GHG emissions from this forest to global warming, an effect that

can persist for several months after the storm. Taken together, our results show that hurricane disturbance in coastal tropical forests can, at least temporarily, shift the radiative forcing of soils in these forests, exacerbating climate change.

Reagan, D.P. 1991. The Response of *Anolis* Lizards to Hurricane-Induced Habitat Changes in a Puerto Rican Rain Forest. Biotropica. 23(4a): 468-474. https://doi.org/10.2307/2388268

The abundance and distribution of anoline lizards were investigated in tabonuco forest in the Luquillo Mountains of Puerto Rico before and for 13 mo following Hurricane Hugo. The drastic reduction in canopy structure immediately following the hurricane confined anole activity to the lower few meters of the forest. *Anolis stratulus*, a canopy species, responded to changes in the distribution of suitable habitat structure while *A. gundlachi*, a forest interior species, apparently responded to changes in microclimate. One year posthurricane, *A. stratulus* had begun reinvasion of the forest canopy, and relative abundances of species at ground level proceeded toward prehurricane values. One year posthurricane, the total anoline minimum density at ground level was still substantially lower than prehurricane levels.

Reed, S.C.; Reibold, R.; Cavaleri, M.A. [and others]. 2020. Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance. Advances in Ecological Research. 62: 225-252. https://doi.org/10.1016/bs.aecr.2020.01.007

Tropical forests represent < 15% of Earth's terrestrial surface yet support > 50% of the planet's species and play a disproportionately large role in determining climate due to the vast amounts of carbon they store and exchange with the atmosphere. Currently, disturbance patterns in tropical ecosystems are changing due to factors such as increased land use pressure and altered patterns in hurricanes. At the same time, these regions are expected to experience unprecedented warming before 2100. Despite the importance of these ecosystems for forecasting the global consequences of multiple stressors, our understanding of how projected changes in climate and disturbance will affect the biogeochemical cycling of tropical forests remains in its infancy. Until now, no studies to our knowledge have evaluated forest recovery following hurricane disturbance within the context of concurrent climatic change. Here, we present soil biogeochemical results from a tropical forest field warming experiment in Puerto Rico where, a year after experimental warming began, Hurricanes Irma and María greatly altered the forest, allowing a unique opportunity to explore the interacting effects of hurricane disturbance and warming. We tracked post-hurricane forest recovery for a year without warming to assess legacy effects of prior warming on the disturbance response, and then reinitiated warming treatments to further evaluate interactions between forest recovery and warmer temperatures. The data showed that warming affected multiple aspects

of soil biogeochemical cycling even in the first year of treatment, with particularly large positive effects on soil microbial biomass pools (e.g., increases of 54%, 33%, and 38% relative to the control plots were observed for microbial biomass carbon, nitrogen, and phosphorus, respectively after 6 months of warming). We also observed significant effects of the hurricanes on soil biogeochemical cycling, as well as interactive controls of warming and disturbance. Taken together, our results showed dynamic soil responses that suggest the future of biogeochemical cycling in this tropical wet forest will be strongly shaped by the directional effects of warming and the episodic effects of hurricanes.

Rice, K.; Brokaw, N.; Thompson, J. 2004. Liana abundance in a Puerto Rican forest. Forest Ecology and Management. 190: 33-41.
https://doi.org/10.1016/j.foreco.2003.10.004

Liana (woody vine) abundance varies among tropical forests and is often high in disturbed forests. In two areas of subtropical wet forest in Puerto Rico, El Verde and Bisley, we recorded the density of liana stems ≥1 cm dbh, and the percent of tree crowns (trees ≥10 cm dbh) that lianas infested. Both study areas have been disturbed by hurricanes several times in the past century; however, sample plots in each area were divided between plots that were less disturbed and those that were more disturbed, by both hurricanes and humans. The mean density and basal area of liana stems at El Verde were significantly higher in the less disturbed plots than in the more disturbed plots. The percent tree crown infested by lianas was higher on certain tree species and on larger trees, both of which characterized the less disturbed forest. Results at Bisley were similar to those at El Verde. Liana density and tree crown infestation in these Puerto Rican forests were low compared with most other tropical forests, contrasting especially with high values in other disturbed forests. Liana abundance varies among forests for complex reasons, including differences in disturbance, biogeography, seasonality, and tree host features.

Richardson, B.A.; Richardson, M.J.; Soto-Adames, F.N. 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. Journal of Animal Ecology. 74(5): 926-936.
https://doi.org/10.1111/j.1365-2656.2005.00990.x
Download: https://www.fs.usda.gov/treesearch/pubs/30082

The primary effects of climatic conditions on invertebrate litter communities, and the secondary effects of different forest types, were distinguished by using the sierra palm as a control in a natural experiment along an elevational gradient in the Luquillo Mountains. These mountains have three well-defined forest types along the gradient, with the palm occurring as stands within each forest. Palm litter samples were richer in nutrients,

particularly phosphorus, than nonpalm litter, significantly so at higher elevations where leaching would have been expected. In nonpalm litter, mineral concentrations were significantly lower at higher elevations. Animal abundance mirrored the pattern of mineral amounts and declined significantly in mid- and high-altitude forests, but did not decline with increasing elevation in palm stands. A pulse of post-hurricane litterfall was reflected in the high abundance of Coleoptera and Isoptera the following year. The species richness of communities (Margalef's index) declined with increasing elevation in nonpalm forest litter, but was remarkably similar in palm litter at all elevations. Palm litter communities were more similar to each other (Sørensen's index) than nonpalm communities, which became less similar with increasing elevation. The differences observed from the lower slopes to the summits, in animal abundance, species richness and the uniformity of communities, are better explained by the contribution of forest composition to the chemical and physical nature of litter and forest heterogeneity, rather than to direct effects of temperature and rainfall differences.

Richardson, B.A.; Richardson, M.J.; González, G. [and others]. 2010. A Canopy Trimming Experiment in Puerto Rico: The Response of Litter Invertebrate Communities to Canopy Loss and Debris Deposition in a Tropical Forest Subject to Hurricanes. Ecosystems. 13: 286-301. https://doi.org/10.1007/s10021-010-9317-6
Download: https://www.fs.usda.gov/treesearch/pubs/36728

Hurricanes cause canopy removal and deposition of pulses of litter to the forest floor. A Canopy Trimming Experiment (CTE) was designed to decouple these two factors, and to investigate the separate abiotic and biotic consequences of hurricane-type damage and monitor recovery processes. As part of this experiment, effects on forest floor invertebrate communities were studied using litterbags. Canopy opening resulted in increased throughfall, soil moisture and light levels, but decreased litter moisture. Of these, only throughfall and soil moisture had returned to control levels 9 months after trimming. Canopy opening was the major determinant of adverse changes in forest floor invertebrate litter communities, by reducing diversity and biomass, irrespective of debris deposition, which played a secondary role. Plots subjected to the most disturbance, with canopy removed and debris added, had the lowest diversity and biomass. These two parameters were higher than control levels when debris was added to plots with an intact canopy, demonstrating that increased nutrient potential or habitat complexity can have a beneficial effect, but only if the abiotic conditions are suitable. Animal abundance remained similar over all treatments, because individual taxa responded differently to canopy trimming. Mites, Collembola, and Psocoptera, all microbiovores feeding mainly on fungal hyphae and spores, responded positively, with higher abundance in trimmed plots, whereas all other taxa, particularly predators and larger

detritivores, declined in relative abundance. Litterbag mesh size and litter type had only minor effects on communities, and canopy trimming and debris deposition explained most variation between sites. Effects of trimming on diversity, biomass, and abundance of some invertebrate taxa were still seen when observations finished and canopy closure was complete at 19 months. This suggests that disturbance has a long-lasting effect on litter communities and may, therefore, delay detrital processing, depending on the severity of canopy damage and rate of regrowth.

Richardson, M.J.; Richardson, B.A.; Srivastava, D.S. 2015. The Stability of Invertebrate Communities in Bromeliad Phytotelmata in a Rain Forest Subject to Hurricanes. Biotropica. 47(2): 201-207. https://doi.org/10.1111/btp.12204

Communities of invertebrate animals in lower canopy and saxicolous tank bromeliads, originally studied in 1993–1997, were resampled along an elevational gradient in tabonuco, palo colorado, and dwarf or cloud forest in Puerto Rico in 2010. These Puerto Rican montane rain forests were impacted strongly by hurricanes in 1989 and 1998, so the surveys in the 1990s represented 4–8 yr of post-hurricane recovery, whereas our recent survey represents 12 yr of post-hurricane recovery. At most elevations, species diversity, both within individual bromeliads and at the forest scale, declined between the 1990s and 2010. This decline in diversity between decades is associated with reductions in bromeliad density as the canopy progressively closed during recovery from hurricane damage. The observed decline in alpha and gamma diversity appears to have involved the loss of rarer species, as might be expected from standard metapopulation theory. By contrast, the most common species were remarkably stable in abundance, composition, and frequency of occurrence over the two decades. In the lowermost tabonuco forest, two endemic bromeliad specialists, restricted to bromeliads for their entire life cycle, were not found on resampling. This study also demonstrates that, at least in Puerto Rico, sets of ten plants from each forest were sufficient to monitor bromeliad invertebrate populations and their diversity over time.

Rivera-Milán, F.F. 1995. Detectability and population density of Scaly-naped Pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island. The Wilson Bulletin. 107(4): 727-733. https://www.jstor.org/stable/4163611

Royo, A.A.; Heartsill Scalley, T.; Moya, S. [and other]. 2011. Non-arborescent vegetation trajectories following repeated hurricane disturbance: Ephemeral versus enduring responses. Ecosphere. 2(7): 77. https://doi.org/10.1890/ES11-00118.1 Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/es11-00118.1

Hurricanes strongly influence short-term patterns of plant community structure, composition, and abundance and are a major contributor to the maintenance of plant diversity in many forests. Although much research has focused on the immediate and long-term effects of hurricane disturbance on tree diversity, far less attention has been devoted to the non-arborescent understory community that often account for the vast majority of the vascular species. Using a unique 20 year dataset, we tracked changes in richness, cover, biomass, and diversity (H′) of non-arborescent species following Hurricane Hugo (1989) and Hurricane Georges (1998) in a mature secondary subtropical wet forest of Puerto Rico. Hurricanes caused an immediate, albeit transient, increase in overall species richness, cover, and diversity. Over a twenty year period, the non-arborescent community exhibited pronounced and persistent changes in composition, including a dramatic increase in abundance and richness of ferns and vines and a concomitant decrease in forbs and shrubs. By 2010, understory composition and relative abundance hierarchies were significantly altered; ferns and vines combined comprised 75 and 90% of total understory cover and biomass, respectively. Our results for this community contrast sharply with prior studies on similar temporal and spatial scales that demonstrate hurricanes rarely alter dominant tree species composition over the long-term. These results suggest that the role of hurricane disturbance in structuring plant diversity may be even more important than previously thought.

Sanford, R.L.; Parton, W.J.; Ojima, D.S. [and other]. 1991. Hurricane Effects on Soil Organic Matter Dynamics and Forest Production in the Luquillo Experimental Forest, Puerto Rico: Results of Simulation Modeling. Biotropica. 23(4a): 364-372.
https://doi.org/10.2307/2388253
Download: https://www.fs.usda.gov/research/treesearch/66369

The forests and soils at Luquillo Experimental Forest (LEF), Puerto Rico, are frequently disturbed by hurricanes occurring at various frequencies and intensities. We have derived a forest version of the Century soil organic matter model to examine the impact of hurricanes on soil nutrient availability and pool sizes, and forest productivity in the tabonuco forest at Luquillo. The model adequately predicted aboveground plant production, soil carbon, and soil nitrogen levels for forest conditions existing before Hurricane Hugo. Simulations of Hurricane Hugo and of an historical sequence of hurricanes indicated a complex pattern of recovery, especially for the first 10 yr after the hurricanes. After repeated hurricanes, forest biomass was reduced, while forest productivity was enhanced. Soil organic matter, and phosphorus and nitrogen mineralization stabilized at higher levels for the LEF than for hurricane-free tabonuco forest, and organic soil phosphorus was substantially increased by hurricanes. Results from these simulations should be regarded as hypotheses. At present there is insufficient data to validate the results of hurricane model simulations.

Scatena, F.N.; Lugo, A.E. 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology. 13: 199-213.
Download: https://www.fs.usda.gov/treesearch/pubs/30266

Relationships between landforms, soil nutrients, forest structure, and the relative importance of different disturbances were quantified in two subtropical wet steepland watersheds in Puerto Rico. Ridges had fewer landslides and treefall gaps, more above-ground biomass, older aged stands, and greater species richness than other landscape positions. Ridge soils had relatively low quantities of exchangeable bases but high soil organic matter, acidity and exchangeable iron. Valley sites had higher frequencies of disturbance, less biomass, younger aged stands, lower species richness and soils with more exchangeable bases. Soil N, P, and K were distributed relatively independently of geomorphic setting, but were significantly related to the composition and age of vegetation. On a watershed basis, hurricanes were the dominant natural disturbance in the turnover of individuals, biomass, and forest canopy. However, turnover by the mortality of individuals that die without creating canopy openings was faster than the turnover by any natural disturbance. Only in riparian areas was forest turnover by treefall gaps faster than turnover by hurricanes. The same downslope mass transfer that links soil forming processes across the landscape also influences the distribution of landslides, treefall gaps, and the structure and composition of the forest. One consequence of these interactions is that the greatest above-ground biomass occurs on ridges where the soil nutrient pools are the smallest. Geomorphic stability, edaphic conditions, and biotic adaptations apparently override the importance of spatial variations in soil nutrients in the accumulation of above-ground biomass at this site.

Scatena, F.N.; Moya, S.; Estrada, C. [and other]. 1996. The First Five Years in the Reorganization of Aboveground Biomass and Nutrient Use Following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica. 28(4a): 424-440. https://doi.org/10.2307/2389086
Download: https://www.fs.usda.gov/treesearch/pubs/30470

Five years after Hurricane Hugo reduced the aboveground biomass by 50 percent in two forested watersheds in the Luquillo Experimental Forest of Puerto Rico, regeneration and growth of survivors had increased the aboveground biomass to 86 percent of the pre-hurricane value. Over the 5 yr, the net aboveground productivity averaged 21.6 $Mg \cdot ha^{-1}yr^{-1}$ and was faster than most plantations and secondary forests in the area. Woodfall and associated nutrient fluxes never attained pre-storm values but by the fifth yr, mean daily total litterfall, and N, P, K, Ca, and Mg fluxes in litterfall were 83, 74, 62, 98, 75, and 81 percent of their pre-disturbance values, respectively. Aboveground nutrient pools of these nutrients ranged from

102 to 161 percent of their pre-disturbance values and were larger after 5 yr because of higher nutrient concentrations in the regeneration compared to the older wood that it replaced. The following sequence of ecosystem reorganization during this first 5 yr period is suggested. An initial period of foliage production and crown development occurred as hurricane survivors re-leafed and herbaceous vegetation and woody regeneration became established. During this period, 75 to 92 percent of the nutrient uptake was retained in the aboveground vegetation and there was a relatively low rate of aboveground carbon accumulation per mole of nutrient cycled. This initial period of canopy development was followed by a peak in aboveground productivity that occurred as early successional species entered the sapling and pole stages. This period was followed by the establishment of the litterfall nutrient cycle and an increase in the net productivity per mole of nutrient cycled. During this 5 yr period, the Bisley forest had some of the lowest withinstand nutrient-use-efficiencies and some of the highest levels of aboveground productivity ever observed in the LEF. The study demonstrates that high levels of productivity and rapid rates of aboveground reorganization can be achieved with rapid within-system cycling and inefficient within-stand nutrient use.

Scatena, F.N.; Silver, W.; Siccama, T. [and others]. 1993. Biomass and Nutrient Content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica. 25(1): 15-27.
https://doi.org/10.2307/2388975
Download: https://www.fs.usda.gov/research/treesearch/66370

The biomass and nutrient content of two steepland watersheds were estimated using allometric equations and nutrient concentrations derived from a subsample of the vegetation. Prior to the passage of Hurricane Hugo in September 1989, the watersheds had a total vegetative biomass of 301 tons/ha, 75 percent of which was aboveground. The total nutrient content of this vegetation was 907, 49, 644, 653, and 192 kg/ha for N, P, K, Ca, and Mg, respectively and varied with topographic setting. Concentrations per unit dry weight of P (0.16), K (2.49), Ca (2.13), and Mg (0.62) in aboveground vegetation were similar to other steepland tropical forests, while the concentration of N (2.9) was greater. Following the passage of Hurricane Hugo, the standing aboveground biomass was reduced to 113 t/ha and the aboveground nutrient content of the forest was reduced 45 to 48 percent.

Schaefer, D.A.; McDowell, W.H.; Scatena, F. [and other]. 2000. Effects of Hurricane Disturbance on Stream Water Concentrations and Fluxes in Eight Tropical Forest Watersheds of the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology. 16: 189-207. https://doi.org/10.1017/S0266467400001358
Download: https://www.fs.usda.gov/treesearch/pubs/30121

Stream water chemistry responds substantially to watershed disturbances, but hurricane effects have not been extensively investigated in tropical regions. This study presents a long-term (2.5–11 y) weekly record of stream water chemistry on eight forested watersheds (catchment basins) in the Luquillo Mountains of Puerto Rico. This includes a period before and at least 2 y after the disturbance caused by the 1989 Hurricane Hugo. Nitrate, potassium and ammonium concentrations increased after the hurricane and remained elevated for up to 2 y. Sulphate, chloride, sodium, magnesium and calcium showed smaller relative significant changes. Average stream water exports of potassium, nitrate and ammonium increased by 13.1, 3.6 and 0.54 kg ha^{-1} y^{-1} in the first post-hurricane year across all watersheds. These represent increases of 119, 182 and 102% respectively, compared to the other years of record. The increased stream outputs of potassium and nitrogen in the first 2 y post-hurricane are equivalent to 3% (potassium) and 1% (nitrogen) of the hurricane-derived plant litter. Effects of hurricanes on tropical stream water potassium and nitrogen can be greater than those caused by canopy gaps or limited forest cutting, but less than those following large-scale deforestation or fire.

Schall, J.J.; Pearson, A.R.; Perkins, S.L. 2000. Prevalence of malaria parasites (*Plasmodium floridense* and *Plasmodium azurophilum*) infecting a Puerto Rican lizard (*Anolis gundlachi*): A nine-year study. Journal of Parasitology. 86(3): 511-515.

The prevalence of malaria parasites was studied in the lizard *Anolis gundlachi* over a 9-yr period at a site in the wet evergreen forest of eastern Puerto Rico. Three forms of the parasite infected the lizards; these were *Plasmodium floridense, Plasmodium azurophilum* in erythrocytes, and *P. azurophilum* in white blood cells. Overall prevalence of infection for 8 samples during the study period was significantly higher for males than females (32% of 3,296 males and 22% of 1,439 females). During the study, the site experienced substantial climatic and physical disturbance including rising temperature, droughts, and hurricanes that severely damaged the forest. Parasite prevalence in the first sample, 8 mo after the massive hurricane Hugo, was slightly, though significantly, lower than for subsequent samples. However, overall prevalence was stable during the 9-yr period. The results show malaria prevalence is more constant at the site than found for 2 studies in temperate forests, and that the Puerto Rico system may be an example of the stable, endemic malaria described by standard models for human malaria epidemiology.

Scholl, M.A.; Bassiouni, M.; Torres-Sánchez, A.J. 2021. Drought stress and hurricane defoliation influence mountain clouds and moisture recycling in a tropical forest. Proceedings of the National Academy of Sciences. 118(7): e2021646118. https://doi.org/10.1073/pnas.2021646118

Mountain ranges generate clouds, precipitation, and perennial streamflow for water supplies, but the role of forest cover in mountain hydrometeorology and cloud formation is not well understood. In the Luquillo Experimental Forest of Puerto Rico, mountains are immersed in clouds nightly, providing a steady precipitation source to support the tropical forest ecosystems and human uses. A severe drought in 2015 and the removal of forest canopy (defoliation) by Hurricane Maria in 2017 created natural experiments to examine interactions between the living forest and hydroclimatic processes. These unprecedented land-based observations over 4.5 y revealed that the orographic cloud system was highly responsive to local land-surface moisture and energy balances moderated by the forest. Cloud layer thickness and immersion frequency on the mountain slope correlated with antecedent rainfall, linking recycled terrestrial moisture to the formation of mountain clouds; and cloud-base altitude rose during drought stress and posthurricane defoliation. Changes in diurnal cycles of temperature and vapor-pressure deficit and an increase in sensible versus latent heat flux quantified local meteorological response to forest disturbances. Temperature and water vapor anomalies along the mountain slope persisted for at least 12 mo posthurricane, showing that understory recovery did not replace intact forest canopy function. In many similar settings around the world, prolonged drought, increasing temperatures, and deforestation could affect orographic cloud precipitation and the humans and ecosystems that depend on it.

Schowalter, T.D. 1994. Invertebrate Community Structure and Herbivory in a Tropical Rain Forest Canopy in Puerto Rico Following Hurricane Hugo. Biotropica. 26(3): 312-319. https://doi.org/10.2307/2388853

The effect of hurricane disturbance on canopy invertebrate communities was studied at the Luquillo Experimental Forest in Puerto Rico. Invertebrate community structure and herbivory were compared among tree species co-occurring in intact forest (standing trees) and canopy gaps. Foliage-bearing branches were collected using a long-handled insect net fitted with a closeable plastic bag. Invertebrates were tabulated and foliage was dried, weighed, and measured for area missing. Lepidoptera, predaceous beetles, and decomposers were significantly more abundant in standing trees; whereas, some sap-sucking arthropods were more abundant in canopy gaps, indicating that these taxa responded to changes in microclimate and/or host condition resulting from disturbance. Herbivory (estimated as leaf area missing) and numbers of several taxa differed significantly among tree species, likely reflecting host preferences based on foliage nutritional quality Species diversity and the gradient of disturbance may have masked disturbance effects.

Schowalter, T.D.; Ganio, L.M. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Ecological Entomology. 24: 191-201. https://doi.org/10.1046/j.1365-2311.1999.00186.x

Canopy invertebrate responses to Hurricane Hugo, tree species, and recovery time were examined at the Luquillo Experimental Forest in Puerto Rico during 1991–92 and 1994–95. Six tree species representing early and late successional stages were examined in paired plots representing severe hurricane disturbance (most trees toppled) and light hurricane disturbance (all trees standing and most branches intact). Hurricane disturbance affected invertebrate abundances significantly. Sap-suckers and molluscs were more abundant, and defoliators, detritivores, and emergent aquatic insects were less abundant in recovering tree-fall gaps than in intact forest during this 5-year period. These changes in functional organisation are consistent with comparable studies of arthropod responses to canopy removal during harvest in temperate forests. Tree species also affected invertebrate abundances significantly, but invertebrate communities did not differ significantly between the three early successional and three later successional tree species. Most taxa showed significant annual variation in abundances, but only two Homoptera species showed a significant linear decline in abundance through time, perhaps reflecting long-term trends during recovery. Leaf area missing, an indicator of herbivore effect on canopy processes, showed significant seasonal and annual trends, as well as differences among tree species and hurricane treatments. Generally, leaf area missing peaked during the wet season each year, but reached its highest levels during an extended drought in 1994. Leaf area missing also tended to be higher on the more abundant tree species in each disturbance treatment. Herbivore abundances and leaf area missing were not related to concentrations of nitrogen, phosphorous, potassium, or calcium in the foliage.This study demonstrated that invertebrate community structure and herbivory are dynamic processes that reflect the influences of host species and variable environmental conditions.

Schowalter, T.D.; Pandey, M.; Presley, S.J. [and others]. 2021. Arthropods are not declining but are responsive to disturbance in the Luquillo Experimental Forest, Puerto Rico. Proceedings of the National Academy of Sciences. 118(2): e2002556117. https://doi.org/10.1073/pnas.2002556117
Download: https://www.pnas.org/doi/10.1073/pnas.2002556117

A number of recent studies have documented long-term declines in abundances of important arthropod groups, primarily in Europe and North America. These declines are generally attributed to habitat loss, but a recent study [B.C. Lister, A. Garcia, Proc. Natl. Acad. Sci. USA 115, E10397-E10406 (2018)] from the Luquillo Experimental Forest (LEF) in Puerto Rico attributed declines to global warming. We analyze arthropod data from the LEF to evaluate long-term trends within the context of hurricane-induced disturbance, secondary succession, and temporal variation in temperature. Our analyses demonstrate that responses to hurricane-induced disturbance and ensuing succession were the primary factors that

affected total canopy arthropod abundances on host trees, as well as walking stick abundance on understory shrubs. Ambient and understory temperatures played secondary roles for particular arthropod species, but populations were just as likely to increase as they were to decrease in abundance with increasing temperature. The LEF is a hurricane-mediated system, with major hurricanes effecting changes in temperature that are larger than those induced thus far by global climate change. To persist, arthropods in the LEF must contend with the considerable variation in abiotic conditions associated with repeated, large-scale, and increasingly frequent pulse disturbances. Consequently, they are likely to be well-adapted to the effects of climate change, at least over the short term. Total abundance of canopy arthropods after Hurricane Maria has risen to levels comparable to the peak after Hurricane Hugo. Although the abundances of some taxa have declined over the 29-y period, others have increased, reflecting species turnover in response to disturbance and secondary succession.

Schowalter, T.D.; Willig, M.R.; Presley, S.J. 2017. Post-Hurricane Successional Dynamics in Abundance and Diversity of Canopy Arthropods in a Tropical Rainforest. Environmental Entomology. 46(1): 11-20. https://doi.org/10.1093/ee/nvw155

We quantified long-term successional trajectories of canopy arthropods on six tree species in a tropical rainforest ecosystem in the Luquillo Mountains of Puerto Rico that experienced repeated hurricane-induced disturbances during the 19-yr study (1991–2009). We expected: 1) differential performances of arthropod species to result in taxon- or guild-specific responses; 2) differences in initial conditions to result in distinct successional responses to each hurricane; and 3) the legacy of hurricane-created gaps to persist despite subsequent disturbances. At least one significant effect of gap, time after hurricane, or their interaction occurred for 53 of 116 analyses of taxon abundance, 31 of 84 analyses of guild abundance, and 21 of 60 analyses of biodiversity (e.g., richness, evenness, dominance, and rarity). Significant responses were ~60% more common for time after hurricane than for gap creation, indicating that temporal changes in habitat during recovery were of primary importance. Both increases and decreases in abundance or diversity occurred in response to each factor. Guild-level responses were probably driven by changes in the abundance of resources on which they rely. For example, detritivores were most abundant soon after hurricanes when litter resources were elevated, whereas sap-suckers were most abundant in gaps where new foliage growth was the greatest. The legacy of canopy gaps created by Hurricane Hugo persisted for at least 19 yr, despite droughts and other hurricanes of various intensities that caused forest damage. This reinforces the need to consider historical legacies when seeking to understand responses to disturbance.

Schowalter, T.D.; Willig, M.R.; Presley, S.J. 2014. Canopy arthropod responses to experimental canopy opening and debris deposition in a tropical rainforest subject to hurricanes. Forest Ecology and Management. 332: 93-102.
https://doi.org/10.1016/j.foreco.2013.12.008
Download: https://www.fs.usda.gov/treesearch/pubs/48451

We analyzed responses of canopy arthropods on seven representative early and late successional overstory and understory tree species to a canopy trimming experiment designed to separate effects of canopy opening and debris pulse (resulting from hurricane disturbance) in a tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER) site in Puerto Rico. We expected that either canopy opening or added debris would result in increased abundances of certain scale insects and other hemipterans, and thereby affect arthropod diversity. Six of thirteen arthropod taxa tested showed significant responses to treatments as main effects or interactions. No taxon responded significantly to trim treatment alone. The red wax scale, *Ceroplastes rubens* (on *Manilkara bidentata*), was significantly less abundant in treatments with added debris than in treatments without added debris, and salticid spiders (on *Sloanea berteroana*) were significantly more abundant in treatments with added debris than in other treatments. Canopy trimming generally did not have a significant effect on assemblage diversity, whereas debris deposition significantly increased diversity on three late successional tree species. A number of significant treatment interactions were observed. Overall, the debris pulse had a greater effect on canopy arthropods than did canopy opening, suggesting that changes in plant condition resulting from nutrient availability associated with debris deposition have a greater effect on canopy arthropods than do the more direct and immediate changes in abiotic conditions resulting from canopy opening.

Secrest, M.F.; Willig, M.R.; Peppers, L.L. 1996. The Legacy of Disturbance on Habitat Associations of Terrestrial Snails in the Luquillo Experimental Forest, Puerto Rico. Biotropica. 28(4a): 502-514. https://doi.org/10.2307/2389092

Despite recent studies of the effect of disturbance on the abundance and distribution of organisms, little research has focused on the legacy of infrequent and large scale disturbances, especially from the perspective of habitat associations of animals. In 1989, Hurricane Hugo caused considerable damage to the Luquillo Experimental Forest of Puerto Rico, with the degree of disturbance strongly affected by topogeographic considerations. We examined the abundance, distribution, and habitat associations of four species of land snail (*Caracolus caracolla*, *Nenia tridens*, *Gaeotis nigrolineata*, *Polydontes acutangula*) in the tabonuco forest at two sites (El Verde and Bisley) which were differentially damaged by the hurricane. Five years after the impact of Hurricane Hugo, significant differences between

sites in density persisted for all snails except *P. acutangula*. Moreover, significant differences in habitat characteristics (central tendency and dispersion) were detected between El Verde and Bisley based on univariate and multivariate analyses of a suite of 31 abiotic and biotic variables. Despite these differences, the basis of habitat association for each snail did not differ between sites. The factors that affected microspatial differences in snail density within sites accounted for differences in density between sites. Insight derived from research conducted at a single location (e.g., El Verde) adequately accounted for patterns of variation at another site (e.g., Bisley), even though differences between sites in the extent and severity of damage were well-documented. We hypothesize that the absence of scale-dependence with regard to habitat selection exists because the association among abiotic and biotic variables (character correlation matrix) within sites was not altered differentially by the hurricane or has recovered to a similar state as a consequence of secondary succession.

Shanley, J.B.; McDowell, W.H.; Stallard, R.F. 2011. Long-term patterns and short-term dynamics of stream solutes and suspended sediment in a rapidly weathering tropical watershed. Water Resources Research. 47(7): w07515.
https://doi.org/10.1029/2010WR009788

The 326 ha Río Icacos watershed in the tropical wet forest of the Luquillo Mountains, northeastern Puerto Rico, is underlain by granodiorite bedrock with weathering rates among the highest in the world. We pooled stream chemistry and total suspended sediment (TSS) data sets from three discrete periods: 1983–1987, 1991–1997, and 2000–2008. During this period three major hurricanes crossed the site: Hugo in 1989, Hortense in 1996, and Georges in 1998. Stream chemistry reflects sea salt inputs (Na, Cl, and SO_4), and high weathering rates of the granodiorite (Ca, Mg, Si, and alkalinity). During rainfall, stream composition shifts toward that of precipitation, diluting 90% or more in the largest storms, but maintains a biogeochemical watershed signal marked by elevated K and dissolved organic carbon (DOC) concentration. DOC exhibits an unusual "boomerang" pattern, initially increasing with flow but then decreasing at the highest flows as it becomes depleted and/or vigorous overland flow minimizes contact with watershed surfaces. TSS increased markedly with discharge (power function slope 1.54), reflecting the erosive power of large storms in a landslide-prone landscape. The relations of TSS and most solute concentrations with stream discharge were stable through time, suggesting minimal long-term effects from repeated hurricane disturbance. Nitrate concentration, however, increased about threefold in response to hurricanes then returned to baseline over several years following a pseudo first-order decay pattern. The combined data sets provide insight about important hydrologic pathways, a long-term perspective to assess response to hurricanes, and a framework to evaluate future climate change in tropical ecosystems.

Sharpe, J.M. 2022. Long-term Studies of Annual Variation in Growth and Reproduction of the Understory Fern *Steiropteris deltoidea* in a Hurricane-prone Rainforest in Puerto Rico. American Fern Journal. 112(4): 251-268.
https://doi.org/10.1640/0002-8444-112.4.251

Two long-term studies were conducted in a rainforest in Puerto Rico that included measurements of leaf and plant functional traits of the common fern species *Steiropteris deltoidea*. A Fern Demography study (1993-2009) compared annual variation and effects of a category 3 hurricane (Georges, 1998) on fertile and sterile leaf traits. A second long-term study (2003-2019), the Canopy Trimming Experiment, evaluated annual variation in growth and reproduction of *S. deltoidea* in response to two experimentally simulated and one category 4 hurricane (Maria, 2017). In the Fern Demography study, differences between fertile and sterile leaf production rates and plant leaf count of *S. deltoidea* were significant while leaf lengths and lifespans did not differ between leaf types. Fertile (but not sterile) leaf production increased three-fold after Hurricane Georges but declined 10-fold by the end of the study. Leaf lifespans of cohorts emerging before and in the three years after Hurricane Georges were significantly shortened by tree and debris fall. Elevated production of fertile leaves and increased plant leaf counts followed the two simulated hurricanes of the Canopy Trimming experiment and two natural hurricanes. *Steiropteris deltoidea* exhibits a level of interannual flexibility in some growth and reproductive traits in response to a changed understory environment that suggests it may be a good indicator species for evaluating microhabitat hurricane effects. Although *S. deltoidea* exhibited resilience, predicted increases in frequency and magnitude of hurricanes in response to climate change may test the limits of life history strategies of rainforest understory ferns.

Sharpe, J.M.; Shiels, A.B. 2014. Understory fern community structure, growth and spore production responses to a large-scale hurricane experiment in a Puerto Rico rainforest. Forest Ecology and Management. 332: 75-86.
https://doi.org/10.1016/j.foreco.2014.01.023
Download: https://www.fs.usda.gov/treesearch/pubs/48452

Ferns are abundant in most rainforest understories yet their responses to hurricanes have not been well-studied. Fern community structure, growth and spore production were monitored for two years before and five years after a large-scale experiment that simulated two key components of severe hurricane disturbance: canopy openness and debris deposition. The canopy was opened by cutting branches above 3 m and the fallen leaf and woody debris was either added to or removed from the forest floor resulting in four treatments that were replicated three times in a factorial design. Of the 16 fern species observed during the experiment 12 were present before treatments were applied. All but two of the 16 species

had densities <250 ha^{-1}; *Thelypteris deltoidea* (2258 ha^{-1}) and *Cyathea borinquena* (1521 ha^{-1}) were by far the most common ferns. Under simulated hurricane conditions (open canopy and debris deposition) abundance levels for both *T. deltoidea* and *C. borinquena* were highly resilient and returned to pre-disturbance conditions within three years; therefore the resident (non-pioneer) fern species continued to dominate after disturbance. However, several other variables had increasing or decreasing responses that had not returned to pre-treatment levels by the fifth and final year of the experiment. Four pioneer species appeared in low abundance almost immediately after the canopy was opened, including three native species that spread via spore germination and the invasive *Nephrolepis brownii* that spread by runners. Debris deposition resulted in high mortality for 7 of 12 fern species, with *C. borinquena* among the species little affected and increases in recruitment following mortality of *T. deltoidea* under open canopy. Individuals of both *T. deltoidea* and *C. borinquena* responded to higher light levels with growth spurts reflected in up to two- to three-fold increases in leaf production and emergence of longer leaves. Spore production rates for both *T. deltoidea* and *C. borinquena* had been low in the undisturbed pre-treatment forest, but more than doubled in the years that followed canopy opening. Hurricane impacts to this tropical forest alter the fern community by (1) debris deposition burying individuals and initially reducing some population sizes, and (2) canopy openness overwhelming the negative effects of debris deposition and stimulating growth and reproduction that can last >5 years. Changes resulting from hurricane disturbance that affect the fern-dominated herbaceous layer may ultimately influence structure and function of the long-term understory plant community and consequently the habitat of litter- and soil-dwelling organisms.

Shiels, A.B.; González, G.; Lodge, D.J. [and other]. 2015. Cascading Effects of Canopy Opening and Debris Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest. BioScience. 65(9): 871-881. https://doi.org/10.1093/biosci/biv111
Download: https://www.fs.usda.gov/treesearch/pubs/49302

Intense hurricanes disturb many tropical forests, but the key mechanisms driving post-hurricane forest changes are not fully understood. In Puerto Rico, we used a replicated factorial experiment to determine the mechanisms of forest change associated with canopy openness and organic matter (debris) addition. Cascading effects from canopy openness accounted for most of the shifts in the forest biota and biotic processes, which included increased plant recruitment and richness, as well as the decreased abundance and diversity of several animal groups. Canopy opening decreased litterfall and litter moisture, thereby inhibiting lignin-degrading fungi, which slowed decomposition. Debris addition temporarily increased tree basal area. Elevated soil solution nitrate was a dominant response after past hurricanes; this effect only occurred in our experiment with simultaneous canopy-opening

and debris treatments. Although debris is an important carbon and nutrient source, short-term responses to cyclonic storms appear to be largely driven by canopy opening.

Shiels, A.B.; Ramírez de Arellano, G.B.; Shields, L. 2022. Invasive rodent responses to experimental and natural hurricanes with implications for global climate change. Ecosphere. 13: e4307. https://doi.org/10.1002/ecs2.4307
Download: https://esajournals.onlinelibrary.wiley.com/doi/epdf/10.1002/ecs2.4307

Hurricanes cause dramatic changes to forests by opening the canopy and depositing debris onto the forest floor. How invasive rodent populations respond to hurricanes is not well understood, but shifts in rodent abundance and foraging may result from scarce fruit and seed resources that follow hurricanes. We conducted studies in a wet tropical forest in Puerto Rico to better understand how experimental (canopy trimming experiment) and natural (Hurricane Maria) hurricane effects alter populations of invasive rodents (*Rattus rattus* [rats] and *Mus musculus* [mice]) and their foraging behaviors. To monitor rodent populations, we used tracking tunnels (inked and baited cards inside tunnels enabling identification of animal visitors' footprints) within experimental hurricane plots (arborist trimmed in 2014) and reference plots (closed canopy forest). To assess shifts in rodent foraging, we compared seed removal of two tree species (*Guarea guidonia* and *Prestoea acuminata*) between vertebrate-excluded and free-access treatments in the same experimental and reference plots, and did so 3 months before and 9 months after Hurricane Maria (2017). Trail cameras were used to identify animals responsible for seed removal. Rat incidences generated from tracking tunnel surveys indicated that rat populations were not significantly affected by experimental or natural hurricanes. Before Hurricane Maria there were no mice in the forest interior, yet mice were present in forest plots closest to the road after the hurricane, and their forest invasion coincided with increased grass cover resulting from open forest canopy. Seed removal of *Guarea* and *Prestoea* across all plots was rat dominated (75%-100% rat-removed) and was significantly less after than before Hurricane Maria. However, following Hurricane Maria, the experimental hurricane treatment plots of 2014 had 3.6 times greater seed removal by invasive rats than did the reference plots, which may have resulted from rats selecting post-hurricane forest patches with greater understory cover for foraging. Invasive rodents are resistant to hurricane disturbance in this forest. Predictions of increased hurricane frequency from expected climate change should result in forest with more frequent periods of grassy understories and mouse presence, as well as with heightened rat foraging for fruit and seed in preexisting areas of disturbance.

Shiels, A.B.; Zimmerman, J.K.; García-Montiel, D.C. [and others]. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. Journal of Ecology. 98(3): 659-673. https://doi.org/10.1111/j.1365-2745.2010.01646.x
Download: https://www.fs.usda.gov/treesearch/pubs/36729

(1) We simulated two key components of severe hurricane disturbance, canopy openness and detritus deposition, to determine the independent and interactive effects of these components on woody plant recruitment and forest structure. (2) We increased canopy openness by trimming branches and added or subtracted canopy detritus in a factorial design. Plant responses were measured during the 4-year study, which followed at least 1year of pre-manipulation monitoring. (3) The physical conditions of canopy openness and detritus deposition in our experiment resembled the responses to Hurricane Hugo, a severe category 4 hurricane that struck this forest in 1989. (4) Canopy detritus deposition killed existing woody seedlings and provided a mechanical barrier that suppressed seedling recruitment. The increase in understorey light caused by canopy trimming stimulated germination from the seed bank and increased seedling recruitment and density of pioneer species several hundred-fold when hurricane debris was absent. Many significant interactions between trimming and detritus deposition were evident from the manner in which seedling density, recruitment and mortality changed over time, and subsequently influenced the composition of woody stems (individuals ≥ 1 cm d.b.h.). (5) When the canopy was trimmed, stem densities increased > 2-fold and rates of recruitment into the stem size class increased >25-fold. Trimming had no significant effect on stem mortality. The two dominant species that flourished following canopy trimming were the pioneer species *Cecropia schreberiana* and *Psychotria berteriana*. Deposition of canopy detritus had little effect on stems, although basal area increased slightly when detritus was added. There were no evident effects of the interactions between canopy trimming and detritus deposition on stems. (6) *Synthesis*. The separate and interactive effects of canopy openness and detritus deposition result in variable short-term trajectories of forest recovery. However, the short interval of increased canopy openness due to hurricane impacts and its influence on the recruitment of pioneer trees is the dominant factor that drives short-term recovery and may alter long-term structure and composition of the forest.

Silver, W.L.; Hall, S.J.; González, G. 2014. Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. Forest Ecology and Management. 332: 47-55. https://doi.org/10.1016/j.foreco.2014.05.018
Download: https://www.fs.usda.gov/treesearch/pubs/47465

Humid tropical forests have the highest rates of litterfall production globally, which fuels rapid nutrient recycling and high net ecosystem production. Severe storm events significantly alter patterns in litterfall mass and nutrient dynamics through a combination of canopy

disturbance and litter deposition. In this study, we used a large-scale long-term manipulation experiment to explore the separate and combined effects of canopy trimming and litter deposition on litterfall rates and litter nutrient concentrations and content. The deposition of fine litter associated with the treatments was equivalent to more than two times the annual fine litterfall mass and nutrient content in control plots. Results showed that canopy trimming was the primary driver of changes in litterfall and associated nutrient cycling. Canopy trimming reduced litterfall mass by 14 Mg ha^{-1} over the 2.5 year post-trim period. Nutrient concentrations increased in some litter fractions following trimming, likely due to a combination of changes in the species and fractional composition of litterfall, and increased nutrient uptake from reduced competition for nutrients. Declines in litterfall mass, however, led to large reductions in litterfall nutrient content with a loss of 143 ± 22 kg N ha^{-1} and 7 ± 0.2 kg P ha^{-1} over the 2.5 year post-trim period. There were no significant effects of litter deposition on litterfall rates or nutrient content, contrary to results from some fertilizer experiments. Our results suggest that large pulsed inputs of nutrients associated with tropical storms are unlikely to increase litterfall production, and that canopy disturbance has large and lasting effects on carbon and nutrient cycling.

Silver, W.L.; Scatena, F.N.; Johnson, A.H. [and others]. 1996. At What Temporal Scales Does Disturbance Affect Belowground Nutrient Pools? Biotropica. 28(4a): 441-457. Download: https://www.srs.fs.usda.gov/pubs/30465

We monitored the effects of both harvesting aboveground biomass and Hurricane Hugo on soil chemical and physical properties, and live and dead root biomass over 6 yr in a subtropical wet forest in Puerto Rico. Our goal was to determine how belowground processes changed at different temporal scales including the immediate period prior to revegetation (9 wk), the intermediate period of initial regrowth (9 mo), and the longer-term reorganization of the vegetation and biogeochemical cycling (6 yr). Harvesting resulted in temporary increases in the availability of exchangeable nutrients, but forest floor and soil nutrient pools had generally returned to pre-harvest values over a 9 wk period. Significant amounts of K moved through the soil over this time period, amounting to 29-46 kg/ha^{-1}, and resulting in a reduction in the size of the exchangeable soil K pool. The hurricane deposited approximately 845 kg/ha^{-1} of forest floor mass and considerable nutrients on the soil surface, and increased soil NO_3-N and exchangeable K pools, but in all cases, pool sizes had returned to pre-hurricane values within 9 mo. Examination of the data on an annual time step over the 6 yr period revealed an increase in soil cation pools and a significant decrease in soil pH. No change in soil organic matter was detected at any time step following the disturbances. Live fine root biomass was dramatically reduced as a result of the hurricane, and was only beginning to show signs of recovery near the end of the 6 yr experiment.

Silver, W.L.; Vogt, K.A. 1993. Fine Root Dynamics Following Single and Multiple Disturbances in a Subtropical Wet Forest Ecosystem. The Journal of Ecology. 81(4): 729-738. https://doi.org/10.2307/2261670

(1) Live and dead fine root biomass and rates of root decomposition were studied prior to and immediately following a localized disturbance (experimental gap creation) and a landscape-level disturbance (Hurricane Hugo) in a lower montane subtropical wet forest in Puerto Rico. The effects of the hurricane on the previously disturbed environment (experimental gaps) were also examined to determine the effects of a multiple disturbance regime. (2) A 40% decline in fine live roots occurred two months following gap creation. Six months following the hurricane, high fine root mortality resulted in a decline of 70-77% of the initial fine live root biomass in the experimental gaps; a similar decline occurred in the control forest. Root decay was slow and 48-65% of the fine root necromass still remained in trench plots after one year. (3) Concentrations of Ca, Mg, K, P and N in fine roots (live plus dead) changed little over the course of one year. The loss of nutrients in live fine roots (kg ha-1) was equivalent to the loss of biomass. (4) In the trench plot experiment, high root mortality resulted in lower concentrations of exchangeable cations in the soil, and a lower pH when compared to soil outside the trench plots. Concentrations of NO3–N were higher in the trench plot soils than in the surrounding soil environment and may have contributed to cation losses. (5) Fine roots in this forest were not greatly diminished following localized disturbances and contributed to nutrient conservation. These root systems were more adversely affected by a landscape-level disturbance and by a multiple disturbance regime. High root mortality following these disturbances may result in significant declines in nutrient availability.

Smith-Martin, C.M.; Muscarella, R.; Ankori-Karlinsky, R. [and others]. 2022. Hurricanes increase tropical forest vulnerability to drought. New Phytologist. 235: 1005-1017. https://doi.org/10.1111/nph.18175

Rapid changes in climate and disturbance regimes, including droughts and hurricanes, are likely to influence tropical forests, but our understanding of the compound effects of disturbances on forest ecosystems is extremely limited. Filling this knowledge gap is necessary to elucidate the future of these ecosystems under a changing climate. We examined the relationship between hurricane response (damage, mortality, and resilience) and four hydraulic traits of 13 dominant woody species in a wet tropical forest subject to periodic hurricanes. Species with high resistance to embolisms (low P-50values) and higher safety margins (SMP50) were more resistant to immediate hurricane mortality and breakage, whereas species with higher hurricane resilience (rapid post-hurricane growth) had high capacitance and P-50 values and lowSMP50. During 26 yr of post-hurricane recovery, we found a decrease in community-weighted mean values for traits associated with greater drought

resistance (leaf turgor loss point, P-50, SMP50) and an increase in capacitance, which has been linked with lower drought resistance. Hurricane damage favors slow-growing, drought-tolerant species, whereas post-hurricane high resource conditions favor acquisitive, fast-growing but drought-vulnerable species, increasing forest productivity at the expense of drought tolerance and leading to higher overall forest vulnerability to drought.

Soto-Parrilla, N.M.; Heartsill-Scalley, T. 2021. Missing the trees for the forest: Post-hurricane understory vegetation in relation to spatial variation. Acta Científica. 32(1-3): 44-54.
Download: https://www.fs.usda.gov/treesearch/pubs/62693

Within a forest, differences in landform spatial variation (i.e., geomorphic settings: valley, slope, and ridge) could affect the species richness and distribution present at a particular site. Previous studies have confirmed that plant species richness and biomass changes after a hurricane and such values can vary among geomorphic settings. Understory vegetation, including ferns, herbs, climbers, graminoids, and shrubs, accounts for more than two thirds of flora in tropical ecosystems, but there is limited information of the effect of hurricanes on these communities. We evaluated the structure and composition of understory vegetation in a post-hurricane forest in relation to geomorphic settings. This study was conducted in El Verde Research Area in the Luquillo Experimental Forest, Puerto Rico. We established 1-m^2 plots within three geomorphic settings: riparian valley, slope, and ridge. Within each plot we identified species, estimated percent of cover, and collected biomass samples. Additionally, we estimated species accumulation curves and analyzed species composition among geomorphic settings using multivariate ordination. The relative species abundance of vegetation life-forms was similar among geomorphic settings, but graminoids and climbers exhibited differences in species composition. Higher forest understory biomass and percent vegetation cover was observed at this immediate post-hurricane period than what was reported pre-hurricane. The understory of valley areas had a more distinct species composition than what was observed among ridge and slope areas. The understory vegetation patterns observed would need to be followed through time and among the landforms to confirm the hurricane disturbances effects at these understory scale.

Steudler, P.A.; Melillo, J.M.; Bowden, R.D. [and other]. 1991. The Effects of Natural and Human Disturbances on Soil Nitrogen Dynamics and Trace Gas Fluxes in a Puerto Rican Wet Forest. Biotropica. 23(4a): 356-363. https://doi.org/10.2307/2388252

We examined the effects of two disturbances (Hurricane Hugo and forest clearcutting) on soil nitrogen dynamics and on the exchanges of N_2O, CO_2 and CH_4 between soils and the

atmosphere of a subtropical wet forest in Puerto Rico. The disturbances resulted in prolonged increases in ammonium pools and short-term increases in rates of net N-mineralization and net nitrification. Nitrous oxide emissions increased following both disturbances. The most dramatic increase was observed 4 mo after clearcutting; N_2O emissions (109 49 µg N/m^2-hr) from the cut plot were about two orders of magnitude higher than emissions from the reference plot (1.71 µg N/m^2-hr). Carbon dioxide emissions from both disturbed plots (mean 102.47 mg C/m^2-hr) were about 30 percent lower than the reference (mean 15 1.28 mg C/m^2-hr). Soils at all sites were generally sinks for CH_4. Methane uptake, however, was suppressed by both disturbances. This suppression may be related to disturbance-induced changes in the nitrogen cycle, as we have previously observed in temperate zone forests.

Stewart, M.M. 1995. Climate Driven Population Fluctuations in Rain Forest Frogs. Journal of Herpetology. 29(3): 437-446. https://doi.org/10.2307/1564995

A deme of *Eleutherodactylus* coqui was followed from 1979 to 1993 at El Verde, Puerto Rico, to determine seasonal and annual variation in numbers and activity patterns. All visible frogs and predatory spiders in a 50 × 2 m transect in the forest were counted for three consecutive nights semi-monthly for two years, then annually or biannually thereafter for a total of 255 evening counts. Ten all-night counts were made at five different times of the year to determine time of maximal activity during the night. Population size varied seasonally, with numbers increasing from June until December followed by a gradual decline until May. The number of adults varied from 1 to 29/100 m^2, whereas the number of juveniles varied from 0 to 221/100 m^2. The maximum single count of all frogs was 244. Counts of >100 juveniles occurred during October through January in the years 1979 to 1982, and in 1989. A marked drop in the numbers of frogs occurred in 1984; from 1979 to 1983, 3-50% of the counts yielded ≥15 adults whereas the maximum count from 1984 until 1989 was 11 adults. The drop in numbers was correlated with an increased number of periods of days with ≤3 mm of rain. Over the period 1979 to 1989, the number of frogs observed was negatively correlated with the longest dry period during the previous year. Population size began to decrease in 1983 and never regained prior levels although numbers were increasing early in 1989 before Hurricane Hugo. Juveniles apparently cannot survive extensive drought, and extended dry periods may be lethal to adults who are inhibited from feeding because of potential desiccation. Predatory ctenid spider populations crashed two years following the decline of frog populations, then disappeared following the hurricane as did other arthropod predators. Rather than total monthly or annual rainfall, it is the distribution of the rain that is important to these subtropical wet forest species.

Sullivan, N.H.; Bowden, W.B.; McDowell, W.H. 1999. Short-Term Disappearance of Foliar Litter in Three Species Before and After a hurricane. Biotropica. 31(3): 382-393. https://doi.org/10.1111/j.1744-7429.1999.tb00380.x

Litter disappearance was examined before (1989) and after (1990) Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico using mesh litterbags containing abscised *Cyrilla racemiflont* or *Dacryodes excelsa* leaves or fresh *Prestoea montana* leaves. Biomass and nitrogen dynamics were compared among: (i) species; (ii) mid- and high elevation forest types; (iii) riparian and upland sites; and (iv) pre- and post-hurricane disturbed environments. Biomass disappearance was compared using multiple regression and negative exponential models in which the slopes were estimates of the decomposition rates subsequent to apparent leaching losses and the y-intercepts were indices of initial mass losses (leaching). *Cyrilla racemiflora* leaves with low nitrogen (0.39%) and high lignin (22.1%) content decayed at a low rate and immobilized available nitrogen. *Dacryodes excelsa* leaves had moderate nitrogen (0.67%) and lignin (16.6%) content, decayed at moderate rates, and maintained the initial nitrogen mass. Prestoea montana foliage had high nitrogen (1.76%) and moderate lignin (16.7%) content and rapidly lost both mass and nitrogen. There were no significant differences in litter disappearance and nitrogen dynamics among forest types and slope positions. Initial mass loss of *C. racemiflora* leaves was lower in 1990 but the subsequent decomposition rate did not change. Initial mass losses and the overall decomposition rates were lower in 1990 than in 1989 for *Dacryodes excelsa*. *Dacryodes excelsa* and *C. racemiflora* litter immobilized nitrogen in 1990 but released 10-15 percent of their initial nitrogen in 1989, whereas *P. montana* released nitrogen in both years (25-40%). Observed differences in litter disappearance rates between years may have been due to differences in the timing of precipitation. Foliar litter inputs during post-hurricane recovery of vegetation in Puerto Rico may serve to immobilize and conserve site nitrogen.

Sun, J.; Ewi, X; Zhou, Y. [and others]. 2022. Hurricanes Substantially Reduce the Nutrients in Tropical Forested Watersheds in Puerto Rico. Forests. 13: 71. https://doi.org/10.3390/f13010071
Download: https://www.mdpi.com/1999-4907/13/1/71/pdf

Because nutrients including nitrogen and phosphorus are generally limited in tropical forest ecosystems in Puerto Rico, a quantitative understanding of the nutrient budget at a watershed scale is required to assess vegetation growth and predict forest carbon dynamics. Hurricanes are the most frequent disturbance in Puerto Rico and play an important role in regulating lateral nitrogen and phosphorus exports from the forested watershed. In this study, we selected seven watersheds in Puerto Rico to examine the immediate and lagged effects of hurricanes on nitrogen and phosphorous exports. Our results suggest that immediate

surges of heavy precipitation associated with hurricanes accelerate nitrogen and phosphorus exports as much as 297 +/- 113 and 306 +/- 70 times than the long-term average, respectively. In addition, we estimated that it requires approximately one year for post-hurricane riverine nitrogen and phosphorus concentrations to recover to pre-hurricane levels. During the recovery period, the riverine nitrogen and phosphorus concentrations are 30 +/-6% and 28 +/- 5% higher than the pre-hurricane concentrations on average.

Teh, Y.A.; Silver, W.L.; Scatena, F.N. 2009. A decade of belowground reorganization following multiple disturbances in a subtropical wet forest. Plant Soil. 323:197-212. https://doi.org/10.1007/s11104-009-9926-z
Download: https://link.springer.com/article/10.1007/s11104-009-9926-z

Humid tropical forests are dynamic ecosystems that experience multiple and overlapping disturbance events that vary in frequency, intensity, and spatial extent. Here we report the results of a 10-year study investigating the effects of forest clearing and multiple hurricanes on ecosystem carbon reservoirs, nutrient pools and vegetation. The aboveground plant community was most heavily affected by multiple disturbances, with the 9-year-old stands showing high rates of hurricane-induced mortality relative to surrounding forest. Belowground pools were less affected. Live fine root biomass fluctuated in response to multiple disturbances, but returned to pre-disturbance levels after 10 years. Soil C was resilient to clearing and hurricanes, probably due to the large pool size and high clay content. Soil P fluctuated over time, declining during periods of rapid plant recovery and growth. With the exception of K, base cations recovered within 2 years following clearing and showed little response to hurricane disturbance.

Thompson, J.; Brokaw, N.; Zimmerman, J.K. [and others]. 2002. Land use history, environment, and tree composition in a tropical forest. Ecological Applications. 12(5): 1344-1363. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/1051-0761%282002%29012%5B1344%3ALUHEAT%5D2.0.CO%3B2
Download: https://www.fs.usda.gov/treesearch/pubs/23111

The effects of historical land use on tropical forest must be examined to understand present forest characteristics and to plan conservation strategies. We compared the effects of past land use, topography, soil type, and other environmental variables on tree species composition in a subtropical wet forest in the Luquillo Mountains, Puerto Rico. The study involved stems > 10 cm diameter measured at 130 cm above the ground, within the 16-ha Luquillo Forest Dynamics Plot (LFDP), and represents the forest at the time Hurricane Hugo struck in 1989. Topography in the plot is rugged, and soils are variable. Historical documents and local

residents described past land uses such as clear-felling and selective logging followed by farming, fruit and coffee production, and timber stand improvement in the forest area that now includes the LFDP. These uses ceased 40-60 yr before the study, but their impacts could be differentiated by percent canopy cover seen in aerial photographs from 1936. Using these photographs, we defined four historic cover classes within the LFDP. These ranged from cover class 1, the least tree-covered area in 1936, to cover class 4, with the least intensive historic land use (selective logging and timber stand improvement). In 1989, cover class 1 had the lowest stem density and proportion of large stems, whereas cover class 4 had the highest basal area, species richness, and number of rare and endemic species. Ordination of tree species composition (89 species, 13 167 stems) produced arrays that primarily corresponded to the four cover classes (i.e., historic land uses). The ordination arrays corresponded secondarily to soil characteristics and topography. Natural disturbances (hurricanes, landslides, and local treefalls) affected tree composition, but these effects did not correlate with the major patterns of species distributions on the plot. Thus, it appears that forest development and natural disturbance have not masked the effects of historical land use in this tropical forest, and that past land use was the major influence on the patterns of tree composition in the plot in 1989. The least disturbed stand harbors more rare and endemic species, and such stands should be protected.

Thompson, J.; Lugo, A.E.; Thomlinson, J. 2007. Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. Plant Ecology. 192: 289-301. https://doi.org/10.1007/s11258-007-9318-5
Download: https://www.fs.usda.gov/treesearch/pubs/29990

Tropical forests are suffering from increasing intensities and frequency of disturbances. As a result, non-native species accidentally introduced or intentionally planted for farming, plantations, and ornamental purposes may spread and potentially invade undisturbed native forest. It is not known if these introduced species will become invasive, as a result of recurrent natural disturbances such as hurricanes. Using data from three censuses (spanning 15 years) of a 16-ha subtropical wet forest plot, we investigated the impact of two hurricanes on populations of plant species that were planted in farms and plantations that were then abandoned and from the natural spread of species introduced into Puerto Rico in the past. The populations of four species (*Citrus paradis, Mangifera indica, Musa* sp., and *Simarouba glauca*) changed little over time. Six species (*Artocarpus altilis, Calophyllum calaba, Genipa americana, Hibiscus pernambucensis, Syzygium jambos,* and *Swietenia macrophylla*) declined between the first two censuses after Hurricane Hugo, then increased again in Census 3 after Hurricane Georges. *Spathodea campanulata* gradually increased from census to census, while *Coffea arabica* declined. These introduced species represent only a small part of the forest

basal area and few show signs of increasing over time. The number of stems per plant, new recruits, and the growth rates of these introduced species were within the ranges of those for native plant species. The mortality rates over both census intervals were significantly lower for introduced species (<5% year^{-1}) than for native ones (15% year^{-1}). Many new recruits established after Hurricane Hugo (prior to this study) had opened the forest canopy and these high mortality rates reflect their death as the canopy recovered. Only *Swietenia macrophylla* and *Syzygium jambos* showed an increase in stem numbers in the closed canopy area of forest that had suffered limited human disturbance in the past. A future increase in frequency of disturbance may enable greater stem numbers of introduced species to establish, while lower-mortality rates compared to native species, may allow them to persist during inter-hurricane intervals. An increase in the population of introduced species, especially for those that grow into large trees, may have an impact on this tropical forest in the future.

Torres, J.A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. Journal of Tropical Ecology. 8(3): 285-298. **https://www.jstor.org/stable/2559733**
Download: https://www.fs.usda.gov/treesearch/pubs/50535

Fifteen species of Lepidoptera occurred in large numbers in spring and early summer after the passage of Hurricane Hugo over the north-east of Puerto Rico. *Spodoptera eridania* (Noctuidae) was the most common of the larvae and fed on 56 plant species belonging to 31 families. All the Lepidoptera fed on early successional vegetation. Some of the plants represent new host plants for these species. The outbreaks appeared to be based on the flush of new foliage that developed in the Luquillo Mountains after the passage of the hurricane. The end of the *S. eridania* outbreak was concurrent with the consumption of its preferred host plants and to an apparent increment in parasitism by ichneumonids (Hymenoptera). Parasitism by tachinids (Diptera) may have contributed to the reduction in abundance of other Lepidoptera species that were temporarily very abundant. Natural enemies of *S. eridania* were recorded for the first time in Puerto Rico.

Tunison, R.; Wood, T.E.; Reed, S.C. [and other]. 2023. Respiratory Acclimation of Tropical Forest Roots in Response to In Situ Experimental Warming and Hurricane Disturbance. Ecosystems. https://doi.org/10.1007/s10021-023-00880-y
Download: https://www.fs.usda.gov/research/treesearch/67347

Climate projections predict higher temperatures and more frequent hurricanes in the tropics. Tropical plants subjected to these stresses may respond by acclimating their physiology. We investigated tropical forest root respiration in response to in situ experimental warming and

hurricane disturbance in eastern Puerto Rico. We measured mass-normalized root specific respiration, root biomass, and root traits at the Tropical Responses to Altered Climate Experiment (TRACE), where understory vegetation is warmed + 4 °C above ambient. Our measurements span 5 years, including before and after two major hurricanes, to quantify root contributions to ecosystem carbon fluxes. Experimental warming did not affect root specific respiration at a standard temperature of 25° (RSR_{25}, mean = 3.89 nmol CO_2 g^{-1} s^{-1}) or the temperature sensitivity of root respiration (Q_{10}, mean = 1.75), but did result in decreased fine-root biomass, thereby decreasing area-based estimations of ecosystem-level root respiration in warmed plots by ~ 35%. RSR_{25} of newer roots, which increased with increasing root nitrogen, showed greater rates 6 months after the hurricanes, but subsequently decreased after 12 months. Root specific respiration did not acclimate to higher temperatures, based on lack of adjustments in either Q10 or RSR_{25} in the warmed plots; however, decreased root biomass indicates the root contribution to soil carbon dioxide efflux was overall lower with warming. Lower root biomass may also limit nutrient and water uptake, having potential negative effects on carbon assimilation. Our results show that warming and hurricane disturbance have strong potential to affect tropical forest roots, as well as ecosystem carbon fluxes.

Umaña, M.N. 2023. The interplay of drought and hurricanes on tree recovery: insights from dynamic and weak functional responses. Proceedings of the Royal Society B-Biological Sciences. 290(2007): 20231732. https://doi.org/10.1098/rspb.2023.1732
Download: https://royalsocietypublishing.org/doi/full/10.1098/rspb.2023.1732

Identifying the functional traits that enable recovery after extreme events is necessary for assessing forest persistence and functioning. However, the variability of traits mediating responses to disturbances presents a significant limitation, as these relationships may be contingent on the type of disturbance and change over time. This study investigates the effects of traits on tree growth-for short and longer terms-in response to two vastly different extreme climatic events (droughts and hurricanes) in a Puerto Rican forest. I found that trees display a dynamic functional response to extreme climatic events. Leaf traits associated with efficient photosynthesis mediated faster tree growth after hurricanes, while trees with low wood density and high water use efficiency displayed faster growth after drought. In the longer term, over both drought and hurricanes, tree size was the only significant predictor of growth, with faster growth for smaller trees. However, despite finding significant trait-growth relationships, the predictive power of traits was overall low. As the frequency of extreme events increases due to climate change, understanding the dynamic relationships between traits and tree growth is necessary for identifying strategies for recovery.

Umaña, M.N.; Arellano, G. 2021. Legacy effects of drought on tree growth responses to hurricanes. Ecography. 44(11): 1686-1697. https://doi.org/10.1111/ecog.05803
Download: https://onlinelibrary.wiley.com/doi/epdf/10.1111/ecog.05803

Natural perturbations, including hurricanes and severe droughts, are becoming more frequent and intense in the tropics, yet our understanding of forest responses to these events is still limited. While the relationships between extreme climatic events and tree mortality are frequently studied, responses of trees that survived such perturbations have been rarely reported. Perturbations and their effects can be quite variable, and trees can respond both positively and negatively to them, depending on their sensitivity and opportunistic behavior. Understanding the potential variation in responses both within and among species is important for building predictions of forest responses. We studied tree growth responses (i.e., changes relative to standard conditions) to hurricanes and drought events in Puerto Rico across six common and broadly distributed species. We examined whether there is a congruence in responses to these contrasting extreme climatic events. We show that trees are particularly susceptible to droughts but display a wide range of responses to hurricanes. Despite the high stochasticity in the impacts of hurricanes, trees that showed reduced growth during previous droughts tend to show reduced growth during the hurricanes as well. Our results demonstrate that trees subjected to different and successive major climatic stresses have consistent declines in their performance. Projected increases in the severity of droughts and tropical storms could have an accumulated, and possibly compound, impact on tree growth. Long-term demographic studies are necessary to understand legacy effects of species responses to extreme climatic perturbations.

Umaña, M.N.; Needham, J.; Forero-Montaña, J. [and others]. 2023. Demographic trade-offs and functional shifts in a hurricane-impacted tropical forest. Annals of Botany. mcad004. https://doi.org/10.1093/aob/mcad004

Background and Aims Understanding shifts in the demographic and functional composition of forests after major natural disturbances has become increasingly relevant given the accelerating rates of climate change and elevated frequency of natural disturbances. Although plant demographic strategies are often described across a slow-fast continuum, severe and frequent disturbance events influencing demographic processes may alter the demographic trade-offs and the functional composition of forests. We examined demographic trade-offs and the shifts in functional traits in a hurricane-disturbed forest using long-term data from the Luquillo Forest Dynamics Plot (LFPD) in Puerto Rico. Methods We analysed information on growth, survival, seed rain and seedling recruitment for 30 woody species in the LFDP. In addition, we compiled data on leaf, seed and wood functional traits that capture the main ecological strategies for plants. We used this information to identify the main axes

of demographic variation for this forest community and evaluate shifts in community-weighted means for traits from 2000 to 2016. Key Results The previously identified growth-survival trade-off was not observed. Instead, we identified a fecundity-growth trade-off and an axis representing seedling-to-adult survival. Both axes formed dimensions independent of resprouting ability. Also, changes in tree species composition during the post-hurricane period reflected a directional shift from seedling and tree communities dominated by acquisitive towards conservative leaf economics traits and large seed mass. Wood specific gravity, however, did not show significant directional changes over time. Conclusions Our study demonstrates that tree demographic strategies coping with frequent storms and hurricane disturbances deviate from strategies typically observed in undisturbed forests, yet the shifts in functional composition still conform to the expected changes from acquisitive to conservative resource-uptake strategies expected over succession. In the face of increased rates of natural and anthropogenic disturbance in tropical regions, our results anticipate shifts in species demographic trade-offs and different functional dimensions.

Uriarte, M.; Canham, C.D.; Thompson, J. [and other]. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs. 74(4): 591-614. https://doi.org/10.1890/03-4031

We present a likelihood-based regression method that was developed to analyze the effects of neighborhood competitive interactions and hurricane damage on tree growth and survival. The purpose of the method is to provide robust parameter estimates for a spatially explicit forest simulator and to gain insight into the processes that drive the patterns of species abundance in tropical forests. We test the method using census data from the 16-ha Luquillo Forest Dynamics Plot in Puerto Rico and describe effects of the spatial configuration, sizes, and species of neighboring trees on the growth and survival of 12 dominant tree species representing a variety of life history strategies. Variation in size-dependent growth and mortality suggests a complex relationship between size, growth, and survival under different regimes of light availability. Crowding effects on growth and survival appear to be idiosyncratic to each individual species, and with the exception of pioneers, there is little commonality among species that share similar life histories. We also explain the implications of differential susceptibility to hurricane damage on species' growth and survival and on their ability to respond to damage to neighboring trees. Tree species in the Luquillo Forest Dynamics Plot differ strikingly in both their susceptibility to hurricane disturbance and the nature of their recovery from wind disturbance, through response of both adult plants and juveniles to enhanced resource availability. At the stand level, intense competitive thinning of densely packed saplings that grew after hurricane damage accounted for the majority of post-hurricane mortality, particularly for shade-intolerant species. At the individual species

level, effects of previous hurricane damage on growth and survival depended primarily on variation in the quantity and quality of hurricane damage sustained by target species and their interaction with life history characteristics of these individual species. Finally, we compare models that make different assumptions about the effects of competing species on tree growth and survival (e.g., equivalence of competitors vs. distinct species-specific effects). Size effects alone could not account for growth and survival for the majority of target species. Our results also demonstrate that competing species have distinct per capita effects on growth of dominant target species. In contrast, we found moderate support for a model that assumed functional equivalence of competitors on survival.

Uriarte, M.; Canham, C.D.; Thompson, J. [and others]. 2005. Seedling recruitment in a hurricane-driven tropical forest: Light limitation, density-dependence and the spatial distribution of parent trees. Journal of Ecology. 93: 291-304.
https://doi.org/10.1111/j.0022-0477.2005.00984.x
Download: https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.0022-0477.2005.00984.x

We used inverse modelling to parameterize spatially-explicit seedling recruitment functions for nine canopy tree species in the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico. We modelled the observed spatial variation in seedling recruitment following Hurricane Georges as a function of the potential number of seedlings at a given location (based on local source trees and the potential contribution of parents from outside of the mapped area) and of light levels and density-dependent mortality during establishment. We adopted the model comparison paradigm and compared the performance of increasingly complex models against a null model that assumes uniform seedling distribution across the plot. Our data supported a model in which parents must reach a threshold size before any seedling production will occur. Once parents attain that size, the relationship between tree diameter and the number of seedlings produced is fairly flat for the majority of species. These results contradict previous analyses that simply assumed a linear relationship between biomass and seedling production and a uniform size threshold for seedling production across species. The majority of species tested supported models that included at least one of a bath term (contribution from non-local trees), conspecific density dependence and light availability after the hurricane. Density dependence shifted the mode of the effective dispersal kernel away from potential parent trees and significantly reduced the number of seedlings established near parent trees. Recruitment from non-local sources accounted for 6–81% of observed seedling recruitment depending upon the tree species. Light availability appeared to divide species into three groups that showed more successful seedling establishment at low (< 5% of full sun), intermediate or high light levels (> 30% full sun). Differences between

individual species in the importance of local vs. bath recruitment and the intensity of density dependence suggest the existence of distinct recruitment syndromes that go beyond the traditional focus of tropical tree life histories. Understanding these syndromes will provide valuable insights into the spatial distribution of tropical tree species and the maintenance of tropical forest diversity.

Uriarte, M.; Canham, C.D.; Thompson, J. [and others]. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. Ecological Monographs. 79(3): 423-443. https://doi.org/10.1890/08-0707.1

Forests are often subject to multiple, compounded disturbances, representing both natural and human-induced processes. Predicting forest dynamics requires that we consider how these disturbances interact to affect species demography. Here we present results of an individual-based, spatially explicit forest simulator that we developed to analyze the compounded effects of hurricane disturbance and land use legacies on the dynamics of a subtropical forest. We used data from the 16-ha Luquillo Forest Dynamics Plot in Puerto Rico, together with a reconstruction of historical wind damage, to parameterize the simulator. We used the model to ask two questions. (1) What are the implications of variation in hurricane frequency and severity for the long-term dynamics of forest composition, diversity, and structure? Both storm severity and frequency had striking effects on forest dynamics, composition, and structure. The periodicity of disturbance also played an important role, with periods of high hurricane activity fostering the establishment of species that may become rare in the absence of severe storms and quiescent periods allowing these species to reach reproductive size. Species responses to hurricane disturbance could not be predicted from their life history attributes. However, species perceived to be primary forest species exhibited low temporal variation in abundance through the simulations. (2) How do hurricanes and legacies from human land use interact to determine community structure and composition? Our results suggest that, over time, regardless of the storm regime, land use legacies will become less apparent but will lead to a forest community that contains a mixture of secondary and primary forest species formerly dominant in areas of different land use. In the long term, hurricane disturbance generated two communities with slightly greater similarity than those not subject to storms. Thus, the inclusion of hurricane disturbance does not alter the prediction that land use legacies in this tropical forest will diminish over time. Our simulations also highlight the contingent effects of human legacies on subsequent community dynamics, including the response to hurricane disturbance, therefore supporting the notion that compounded disturbances can interact in ways that cannot be predicted by the study of single disturbances. The widespread importance of land use as a large-scale disturbance makes it imperative that it be addressed as a fundamental ecological process.

Uriarte, M.; Clark, J.S.; Zimmerman, J.K. [and others]. 2012. Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. Ecology. 93(1): 191-205. https://doi.org/10.1890/10-2422.1

Species employ diverse strategies to cope with natural disturbance, but the importance of these strategies for maintaining tree species diversity in forests has been debated. Mechanisms that have the potential to promote tree species coexistence in the context of repeated disturbance include life history trade-offs in colonization and competitive ability or in species' ability to survive at low resource conditions and exploit the temporary resource-rich conditions often generated in the wake of disturbance (successional niche). Quantifying these trade-offs requires long-term forest monitoring and modeling. We developed a hierarchical Bayes model to investigate the strategies tree species employ to withstand and recover from hurricane disturbance and the life history trade-offs that may facilitate species coexistence in forests subject to repeated hurricane disturbance. Unlike previous approaches, our model accommodates temporal variation in process error and observations from multiple sources. We parameterized the model using growth and mortality data from four censuses of a 16-ha plot taken every five years (1990–2005), together with damage data collected after two hurricanes and annual seed production data (1992–2005). Species' susceptibilities to hurricane damage as reflected by changes in diameter growth and fecundity immediately following a storm were weak, highly variable, and unpredictable using traditional life history groupings. The lower crowding conditions (e.g., high light) generated in the wake of storms, however, led to greater gains in growth and fecundity for pioneer and secondary-forest species than for shade-tolerant species, in accordance with expectation of life history. We found moderate trade-offs between survival in high crowding conditions, a metric of competitive ability, and long-distance colonization. We also uncovered a strong trade-off between mean species fecundity in low crowding conditions, a metric of recovery potential, and competitive ability. Trade-offs in competitive and colonization ability, in addition to successional niche processes, are likely to contribute to species persistence in these hurricane-impacted forests. The strategies species employ to cope with hurricane damage depend on the degree to which species rely on sprouting, repair of adult damage, changes in demographic rates in response to enhanced resource availability after storms, or long-distance dispersal as recovery mechanisms.

Uriarte, M.; Tang, C.L.; Morton, D.C. [and others]. 2023. 20th-Century hurricanes leave long-lasting legacies on tropical forest height and the abundance of a dominant wind-resistant palm. Ecology and Evolution. 13(11): e10776.
https://doi.org/10.1002/ece3.10776
Download: https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.10776

Projected increases in hurricane intensity under a warming climate will have profound effects on many forest ecosystems. One key challenge is to disentangle the effects of wind damage from the myriad factors that influence forest structure and species distributions over large spatial scales. Here, we employ a novel machine learning framework with high-resolution aerial photos, and LiDAR collected over 115 km² of El Yunque National Forest in Puerto Rico to examine the effects of topographic exposure to two hurricanes, Hugo (1989) and Georges (1998), and several landscape-scale environmental factors on the current forest height and abundance of a dominant, wind-resistant species, the palm *Prestoea acuminata var. montana*. Model predictions show that the average density of the palm was 32% greater while the canopy height was 20% shorter in forests exposed to the two storms relative to unexposed areas. Our results demonstrate that hurricanes have lasting effects on forest canopy height and composition, suggesting the expected increase in hurricane severity with a warming climate will alter coastal forests in the North Atlantic.

Uriarte, M.; Thompson, J.; Zimmerman, J.K. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. Nature Communications. 10: 1362. https://doi.org/10.1038/s41467-019-09319-2
Download: https://www.nature.com/articles/s41467-019-09319-2#citeas

Tropical cyclones are expected to intensify under a warming climate, with uncertain effects on tropical forests. One key challenge to predicting how more intense storms will influence these ecosystems is to attribute impacts specifically to storm meteorology rather than differences in forest characteristics. Here we compare tree damage data collected in the same forest in Puerto Rico after Hurricanes Hugo (1989, category 3), Georges (1998, category 3), and María (2017, category 4). María killed twice as many trees as Hugo, and for all but two species, broke 2- to 12-fold more stems than the other two storms. Species with high density wood were resistant to uprooting, hurricane-induced mortality, and were protected from breakage during Hugo but not María. Tree inventories and a wind exposure model allow us to attribute these differences in impacts to storm meteorology. A better understanding of risk factors associated with tree species susceptibility to severe storms is key to predicting the future of forest ecosystems under climate warming.

Van Beusekom, A.E.; González, G.; Rivera, M.M. 2023. Tropical Forest Microclimatic Changes: Hurricane, Drought, and 15–20 Year Climate Trend Effects on Elevational Gradient Temperature and Moisture. Forests. 14: 325.
https://doi.org/10.3390/f14020325
Download: https://www.mdpi.com/1999-4907/14/2/325

The effects of hurricanes Irma and Maria and a severe drought on the temperature, precipitation, and soil moisture (under canopy and in the open) were calculated at 22 sites from 0-1045 m in northeastern Puerto Rico from 2001-2021, against the background short-term trend. Median and minimum air temperatures increased uniformly across the elevational gradient, 1.6 times as fast in the air under the canopy (+0.08 degrees C/yr) and 2.2 times as fast in the soil under the canopy (+0.11 degrees C/yr) as for air temperature in the open. There were no substantial moisture trends (average decrease <0.01 mm/yr). The peak effect of the hurricanes on under-canopy air temperature was the same as under-canopy soil temperature at 1000 m (+3, 0.7, 0.4 degrees C for maximum, median, minimum) but air maximum and minimum temperature peak effects were twice as high at 0 m (and soil temperatures stayed constant). Soil temperature hurricane recovery took longer at higher elevations. The peak effect of the hurricanes and the drought on the soil moisture was the same (but in opposite directions, +/- 0%), except for the wettest months where drought peak effect was larger and increasing with elevation. Differing patterns with elevation indicate different ecosystem stresses.

Van Beusekom, A.E.; González, G.; Stankavich, S. [and others]. 2020. Understanding tropical forest abiotic response to hurricanes using experimental manipulations, field observations, and satellite data. Biogeosciences. 17(12): 3149-3163.
https://doi.org/10.5194/bg-17-3149-2020
Download: https://www.fs.usda.gov/treesearch/pubs/60352

With projected increasing intensity of hurricanes and large uncertainty in the path of forest recovery from hurricanes, studies are needed to understand the fundamental response of forests to canopy opening and debris deposition: the response of the abiotic factors underneath the canopy. Through two manipulative experiments and instrumenting prior to Hurricane Maria (2017) in the Luquillo Experimental Forest (LEF) of Puerto Rico, this study found a long recovery time of primary abiotic factors (beneath canopy light, throughfall, and temperature) influenced by the disturbance of canopy opening, as well as complex responses by the secondary abiotic factors (relative humidity, soil moisture, and leaf saturation) influenced by the disturbance of the primary factors. Recovery took 4–5 years for beneath canopy light, while throughfall recovery took 4–9 years and neither had recovered when Hurricane Maria passed 3 years after the second experiment. Air and soil temperature seemingly recovered quickly from each disturbance (<2.5 years in two experiments for ~+1 ^{o}C of change); however, temperature was the most important modulator of secondary factors, which followed the long-term patterns of the throughfall. While the soil remained wetter and relative humidity in the air stayed lower until recovery, leaves in the litter and canopy were wetter and drier, with evidence that leaves dry out faster in low rainfall and saturate faster

in high rainfall after disturbance. Comparison of satellite and field data before and after the 2017 hurricanes showed the utility of satellites in expanding the data coverage, but the muted response of the satellite data suggests they measure dense forest as well as thin forest that is not as disturbed by hurricanes. Thus, quick recovery times recorded by satellites should not be assumed representative of all the forest. Data records spanning the multiple manipulative experiments followed by Hurricane Maria in the LEF provide evidence that intermediate hurricane frequency has the most extreme abiotic response (with evidence on almost all abiotic factors tested) versus infrequent or frequent hurricanes.

Vargas, A.J. 2000. Effects of fertilizer addition and debris removal on leaf-litter spider communities at two elevations. The Journal of Arachnology. 28(1): 79-89. https://doi.org/10.1636/0161-8202(2000)028[0079:EOFAAD]2.0.CO;2

This study investigates the indirect effects of primary productivity enhancement via fertilization, and the direct effects of environmental differences at two elevations, on the density and species richness of leaf-litter spiders. Litter was sampled in tabonuco forest (340–360 m elevation) and elfin forest (1051 m elevation) within the Luquillo Experimental Forest Long Term Ecological Research (LTER) site in Puerto Rico. Treatments consisted of three blocks with fertilization and control plots at both sites, and a one time removal of hurricane generated debris at tabonuco forest only. Treatments had no significant effect on spider density, species diversity, and species richness at either elevation. Elfin forest showed lower densities and lower species richness than tabonuco forest due to harsh environmental conditions. The thin litter layer and similar standing litter in the tabonuco forest suggest that spiders are limited by habitat, and also that they have successfully recolonized the debris cleared areas at this elevation. Harsh environmental conditions at elfin forest seem to be strong enough to counteract the effects of fertilizer addition on the measured variables. However, the high biomass of grasses in the fertilization plots at elfin forest could have caused an underestimation of spider densities. This study suggests that habitat availability is an important variable in bottom-up models for food web link control.

Vogt, K.A.; Vogt, D.J.; Boon, P. [and others]. 1996. Litter Dynamics Along Stream, Riparian and Upslope Areas Following Hurricane Hugo, Luquillo Experimental Forest, Puerto Rico. Biotropica. 28(4a): 458-470. https://doi.org/10.2307/2389088

Litterfall (fine and coarse) due to Hurricane Hugo and subsequent fine annual litterfall inputs (1, 2 and 5 yr after Hugo) were determined for two sites (El Verde and Bisley) in the Luquillo Experimental Forest in Puerto Rico. Litter transfers into streams, riparian and upslope areas were determined within each catchment. The recovery rate of aboveground fine litterfall

(leaf, fine wood <1 cm diameter, and other miscellaneous inputs) to predisturbance levels were determined 1, 2, and 5 yr after Hurricane Hugo. The amount of total litter transfers and their individual components into the riparian and upslope areas due to Hurricane Hugo varied significantly by catchments within the Luquillo Experimental Forest. At El Verde, 26-39 percent, 31-35 percent, 14-35 percent and 7-12 percent of the total litter transfers were contributed by leaf litter, fine wood, coarse wood and fine roots, respectively. At Bisley, 28-31 percent, 26-29 percent, 33-35 percent and 8-10 percent of the litter transfers were contributed by the same categories. Differential decay rates contributed to the relative importance of fine and coarse litter inputs. The recovery of fine aboveground litterfall to pre-hurricane levels after 5 yr varied by topographic location (streams had the slowest recovery, upslope areas the highest) and catchment (El Verde: 55-77%; Bisley: 39-82% of pre-hurricane values).

Wadsworth, F.H.; Englerth, G.H. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. Caribbean Forester. 20: 38-51.
Download: https://www.fs.usda.gov/research/treesearch/66371

Waide, R.B. 1991. The Effect of Hurricane Hugo on Bird Populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica. 23(4a): 475-480.
https://doi.org/10.2307/2388269

Hurricane Hugo caused severe but short-term disruption of the avian community of a subtropical wet forest site in the Luquillo Mountains of Puerto Rico. Nectarivorous and frugivorous bird species were greatly reduced in numbers immediately after the hurricane. The single granivore species studied decreased in numbers more slowly. Insectivores and omnivores increased after the hurricane. All species except the granivore returned to their prehurricane abundance levels prior to the following breeding season, suggesting that population changes were a result of movement in search of food rather than mortality. Mist net captures and observations indicated that birds occupied a reduced vertical foraging range after the hurricane, and stomach contents from birds captured 6-10 months after the hurricane showed that different foods were being consumed. Fewer and different kinds of arthropods were found in stomachs after the hurricane. These findings, coupled with the frequent occurrence of hurricanes in the Caribbean, suggest that there is pressure on bird populations in this region to maintain plasticity in habitat and dietary requirements.

Walker, L.R. 2000. Seedling and Sapling Dynamics of Treefall Pits in Puerto Rico. Biotropica. 32(2): 262-275. https://www.jstor.org/stable/2663855
Download: https://www.fs.usda.gov/treesearch/pubs/30123

Seedling and sapling dynamics in a Puerto Rican rain forest were compared between forest understory and soil pits created by the uprooting of 27 trees during Hurricane Hugo. Soil N and P, organic matter, and soil moisture were lower and bulk densities were higher in the disturbed mineral soils of the pits than in undisturbed forest soils ten months after the hurricane. No differences in N and P levels were found in pit or forest soils under two trees with N-fixing symbionts (*Inga laurina* and *Ormosia krugii*) compared to soils under a tree species without N-fixing symbionts (*Casearia arborea*), but other soil variables (Al, Fe, K) did vary by tree species. Forest plots had greater species richness of seedlings (<10 cm tall) and saplings (10-100 cm tall) than plots in the soil pits (and greater sapling densities), but seedling densities were similar between plot types. Species richness and seedling densities did not vary among plots associated with the three tree species, but some saplings were more abundant under trees of the same species. Pit size did not affect species richness or seedling and sapling densities. Recruitment of young *Cecropia schreberiana* trees (>5 m tall) 45 months after the hurricane was entirely from the soil pits, with no tree recruitment from forest plots. Larger soil pits had more tree recruitment than smaller pits. Defoliation of the forest by the hurricane created a large but temporary increase in light availability. Recruitment of *C. schreberiana* to the canopy occurred in gaps created by the treefall pits that had lower soil nutrients but provided a longer-term increase in light availability. Treefall pits also significantly altered the recruitment and mortality of many understory species in the Puerto Rican rain forest but did not alter species richness.

Walker, LR. 1995. Timing of post-hurricane tree mortality in Puerto Rico. Journal of Tropical Ecology. 11: 315-320. https://doi.org/10.1017/S0266467400008786

Walker, L.R. 1991. Tree Damage and Recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica. 23(4a): 379-385. https://doi.org/10.2307/2388255

Hurricane Hugo struck Puerto Rico on 18 September 1989 with maximum sustained winds of over 166 km/hr (Scatena & Larsen 1991) and caused severe defoliation of 56 percent of the trees in study plots at El Verde in the Luquillo Experimental Forest (LEF). Some trees were uprooted (9%) or had trunks that snapped (11%), but overall mortality was low (7%). Damage was patchy on twenty 300 m2 plots with most damage occurring on north-facing sites. Tall trees and trees with large diameters were most likely to be uprooted, but successional status of trees was not a good predictor of the amount of damage the trees sustained. Recovery patterns varied among species but refoliation was rapid. Widespread sprouting and minimal breakage of large branches will probably lead to the recovery of most trees.

Walker, L.R.; Lodge, D.J.; Guzmán-Grajales, S.M. [and other]. 2003. Species-Specific Seedling Responses to Hurricane Disturbance in a Puerto Rican Rain Forest. Biotropica. 35(4): 472-485. https://doi.org/10.1111/j.1744-7429.2003.tb00604.x
Download: https://www.fs.usda.gov/treesearch/pubs/30188

Seedling dynamics were followed in a Puerto Rican forest for 20 months following a severe hurricane to study the interactive effects of hurricane debris, nutrients, and light on seedling diversity, density, growth, and mortality. Three treatments (debris removal, an unaltered control with hurricane debris, and chemical fertilization added to hurricane debris) altered levels of forest debris and soil nutrients. Canopy openness was measured twice using hemispherical photographs of the canopy. We examined the demographic responses of six common species to treatments over time. Seedling densities increased for all six species but the only significant treatment effects were increased densities of the pioneer tree *Cecropia* and the shrub *Palicourea* in the debris removal treatment. Seedling growth declined with declining light levels for four species but not for the pioneer tree *Alchornea* or the non-pioneer tree *Dacryodes*. Only *Cecropia* and the non-pioneer tree *Chionanthus* had treatment effects on growth. Mortality also differed among species and tended to be highest in the fertilized plots for all but *Cecropia* and *Dacryodes*. We found only some of the expected differences between pioneer and non-pioneer plants, as each species had a unique response to the patchy distributions of organic debris, nutrients, and light following the hurricane. High local species diversity was maintained through the individualistic responses of seedlings after a disturbance.

Walker, L.R.; Neris, L.E. 1993. Posthurricane Seed Rain Dynamics in Puerto Rico. Biotropica. 25(4): 408-418. https://doi.org/10.2307/2388864

Seed rain was measured in the center (open habitat) and at the edges of two recent landslides and in adjacent subtropical wet forest in eastern Puerto Rico. We trapped seeds for 2 yr after the trees in the forest were severely damaged by Hurricane Hugo. The number of seeds trapped per fortnight did not increase with time. Cumulative numbers of species were highest in the edge habitat during the first year but highest in the forest during the second year. Seeds from shrubs dominated the seed rain and also had the highest germination under shadehouse conditions (shrubs > vines > trees > herbs). The dominance of the seed rain by shrubs was apparently due to increased fruit production of existing understory shrubs in the forest after canopy removal by the hurricane, and to colonizing shrubs on the landslides. Peaks of seed rain coincided with short periods of high seed production by plants in the vicinity of individual traps. Despite large spatial variability, the seed rain did represent the local flora and long distance dispersal was not necessary to explain seed rain dynamics.

Walker, L.R.; Voltzow, J.; Ackerman, J.D. [and others]. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. Ecology. 73(2): 691-694. https://doi.org/10.2307/1940775

Walker, L.R.; Zimmerman, J.K.; Lodge, D.J. [and other]. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. Journal of Ecology. 84: 877-889. https://doi.org/10.2307/2960559
Download: https://www.fs.usda.gov/research/treesearch/66372

(1) The controls over above-ground primary productivity following hurricane damage were investigated in a lowland subtropical wet forest (350-500 m altitude) and a lower montane elfin forest (1050 m) in Puerto Rico. Responses of understorey and canopy vegetation to addition of a complete nutrient fertilizer (both altitudes) or hurricane debris removal (lowland only) were monitored for 47-50 months. Treatments were initiated 1-6 months after Hurricane Hugo severely damaged both forests (18 September 1989). (2) Fertilization stimulated leaf litter production in both forests, but the recovery to prehurricane levels occurred earlier in the lowland forest (20 months after initiation of treatment) than in the elfin forest (38 months). Debris removal also increased leaf litter production in the lowland forest. (3) Tree diameter growth was 10-fold greater at low than at high altitude but the only treatment effect was a time by treatment interaction in the lowland forest, indicating that diameters of trees in the debris removal treatment did not increase as rapidly as in the control of fertilizer treatments. (4) Fertilization altered understorey biomass in the elfin forest (graminoids increased 10-fold, bryophytes decreased three-fold) but not in the lowland forest. Debris removal had no effect on understorey biomass in the lowland forest although woody seedling densities were highest in the debris removal plots. In control plots, understorey biomass was 12-fold greater at high than at low altitude. Saplings of a pioneer tree, *Cecropia schreberiana* were three- to five-fold denser in fertilized plots than in control or debris removal plots in the lowland forest. (5) The study showed that establishment of woody species by seeds was more important to posthurricane regeneration in the lowland than in the elfin forest and that the recovery of forest productivity was less responsive to increased nutrient availability in the elfin forest. Opportunistic, rapid responses to nutrient addition by *Cecropia* (low altitude) or graminoids (both high and low altitude) contrasted with the relatively slow responses of mature forest trees. These results suggest that factors regulating primary productivity following disturbance are influenced not only by the physical characteristics of the site but also by the range of potential species-specific responses represented in the flora.

Wang, H.; Hall, C.A.S. 2004. Modeling the effects of Hurricane Hugo on spatial and temporal variation in primary productivity and soil carbon and nitrogen in the Luquillo Experimental Forest, Puerto Rico. Plant Soil. 263: 69-84.
https://doi.org/10.1023/B:PLSO.0000047719.44971.dd

Hurricanes account for much of the spatial and temporal variation in forest productivity and soil organic matter pools in many forest ecosystems. In this study, we used an ecosystem level model, TOPOECO, to simulate the effects of Hurricane Hugo (18 September 1989) on spatial and temporal patterns of gross primary productivity (GPP), net primary productivity (NPP), soil organic carbon (SOC) and nitrogen over the entire Luquillo Experimental Forest (LEF), Puerto Rico, a tropical rainforest. Our simulation results indicated that simulated annual GPP increased by an average of 30% five years after Hugo in the Tabonuco forest at low elevations where there was a fast recovery of the canopy, whereas simulated GPP decreased by an average of 20% in the Palm and Dwarf forests at high elevations as a result of the slow recovery of the canopy. Simulated annual NPP in the Palm and Dwarf forests also did not recover to pre-Hugo levels within 5 years. Simulated storages of SOC, CO_2 emission from decomposition of SOC and total soil nitrogen increased slightly but N mineralization rate increased significantly in all four vegetation types due to the massive input of plant materials from Hugo at low elevations and the slow decomposition at high elevations.

Weaver, P.L. 2013. Long-term changes in structure and composition following hurricanes in a primary lower montane rain forest in Puerto Rico. Bois et Forêts des Tropiques. 317(3): 7-20.
Download: https://www.fs.usda.gov/research/treesearch/46989

Ridges within the lower montane rain forests (sensu Beard) of the Caribbean Basin are dominated by *Dacryodes excelsa*, a tree species known as tabonuco in Puerto Rico and gommier in the Lesser Antilles. Periodially, hurricanes traverse the islands causing changes in structure, species composition, and dynamics of forests. The chronology of post-hurricane vegetation change from 1946 to 2010 on a 0.4 ha ridge plot approximately 380 m in elevation in the Luquillo Experimental Forest of northeastern Puerto Rico showed: (1) defoliation, breakage, and uprooting by wind accompanied by immediate mortality resulting in a loss in forest structure, including stem numbers, tree height, and biomass; (2) delayed mortality of some impacted trees, along with prompt, abundant ingrowth of *Cecropia schreberiana*, and the other secodary species, increasing the number of stems within the forest; (3) a post-hurricane increase in diamater growth and biomass accumulation for approximately 20 years, followed by a decline in both rates; (4) a high post-hurricane survival and increase in dbh increment of *Dacryodes excelsa*; (5) a post-hurricane increase in species richness for 20 years when

primary and secondary species grow together, followed by a decline due to competition; (6) asymptomatic conditions for stems, biomass, and number of species after more than 40 years. In addition, related studies in the same forest type showed that hurricanes and thinning evoke comparable growth responses. This study should be of regional interest because Puerto Rico's lower montane rain forest shares similar environmental conditions as well as tree species with the mountainous Antilles.

Weaver, P.L. 2008. Dwarf Forest Recovery after Disturbances in the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science. 44(2): 150-163.
Download: https://www.fs.usda.gov/treesearch/pubs/35425

Dwarf forest in Puerto Rico's Luquillo Mountains varies according to substrate and topography with very short, dense forest growing on exposed, rocky sites. High elevation level sites suffered considerable damage during past hurricanes whereas the trees on certain lower slopes were protected by ridges or spurs. Post-disturbance recovery of dwarf forest on two types of sample plots near East Peak was slow. Nearly 37 years after a 1968 airplane crash, *Cyathea bryophila* (R. Tryon) Proctor and *Eugenia borinquensis* Britton accounted for 71% of the 25.3 t ha^{-1} total aboveground dry weight biomass (hereafter biomass) on 780 m^2 of the crash site. This is only 30% of the 80 t ha^{-1} average biomass of the surrounding dwarf forest prior to Hurricane Hugo of 1989. Also, six 250 m^2 permanent plots (stratified by topography with sites on ridges, slopes, and ravines) showed delayed post-hurricane mortality, declining in mean stem numbers from 2,956 stems ha−1 in 1990 to 2,268 stems ha^{-1} in 2005. Average plot biomass decreased from 72.8 t ha^{-1} in 1990 to 61.6 t ha^{-1} in 2000, increasing slightly to 62.9 t ha^{-1} in 2005. Recovery on all sites was characterized by an immediate invasion of grass cover along with an influx of ferns, followed by dicotyledonous seedlings and saplings, and finally small trees. More than one-half of the arborescent species growing in dwarf forest are endemic to Puerto Rico where they play a prominent role in post disturbance recovery; moreover, 85% of the trees do not exceed 15 m in height anywhere in the Luquillo Mountains.

Weaver, P.L. 2002. A chronology of hurricane induced changes in Puerto Rico's Lower Montane Rain Forest. Interciencia. 27(5): 252-258.
Download: https://www.fs.usda.gov/research/treesearch/66373

Ridges in the lower montane rain forests of Puerto Rico and the Lesser Antilles from St. Kitts to Grenada are dominated by tabonuco (*Dacryodes excelsa* Vahl), a long-lived tree adapted to recurrent hurricanes. The oldest tabonuco trees in Puerto Rico appear to survive 500 to 600yrs in forests that periodically (perhaps every 50 to 60yrs) lose nearly one-fifth of their biomass. Post hurricane-recovery, characterized by greater rates of stem ingrowth and mortality,

showed an immediate and abundant regeneration of yagrumo hembra (*Cecropia schreberiana* Mig.) along with numerous small- to medium-sized species in forest openings. Stem density, species numbers, and the rate of biomass accumulation are at a maximum 15yrs after the hurricane; about 50yrs later, most of the secondary species associated with past forest disturbance have disappeared and the rate of biomass accumulation becomes asymptotic.

Weaver, P.L. 1999. Impacts of Hurricane Hugo on the Dwarf Cloud Forest of Puerto Rico's Luquillo Mountains. Caribbean Journal of Science. 35(1-2): 101-111.
Download: https://www.fs.usda.gov/research/treesearch/66374

Stratified sampling by topography in the dwarf cloud forest of the Luquillo Experimental Forest indicated that many common tree species showed topographic preferences, favoring either ravines or slopes and ridges. Delayed post-hurricane mortality (≥1.3 and ≤6.3 yrs) on permanent plots established after the passage of Hurricane Hugo in September 1989 reduced the number of stems on Pico del Este by 21%, most notably impacting the smallest dbh and height classes in ridges. Mortality varied by species, with the palm *Prestoea montana* (R. Grah.) Nichols showing the best survival and the tree *Clusia closoides* (Griseb.) D'Arcy the poorest. Regressions of epiphytic biomass expressed as a function of bole dbh or crown area did not correlate as well in post-hurricane conditions as they did in pre-hurricanes conditions. Although total litterfall was virtually the same, the leafy fraction declined and the woody fraction increased. Tree mortality decreased aboveground biomass after the storm. Total aboveground net primary productivity sampled from 1.3 to 2.3 yrs after Hugo was 20% greater than before the storm when 5-yr estimate of average coarse debris (from 1.3 to 6.3 years post-hurricane) was added.

Weaver, P.L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. Interciencia. 14(4): 181-192.
Download: https://www.fs.usda.gov/research/treesearch/66375

Weaver, P.L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science. 22(1-2): 53-70.
Download: https://www.fs.usda.gov/research/treesearch/66376

Periodic disturbances caused by hurricanes constitute an integral phase of forest growth and development in the Caribbean region. The 35-year recovery in seven permanent plots in the Colorado Forest of the Luquillo Mountains in Puerto Rico covering the 14 through 49 year period after a major disturbance was characterized by: (1) ingrowth and mortality rates of 20 stems/ha/yr, or 1.1% yr of the initial number of stems; (2) shifts to larger tree diameters

and heights; (3) a 3% decline in the number of trees in the intermediate and dominant crown classes and a 6% increase in the number of suppressed trees; (4) a 1.1% increase in the weighted mean specific gravity of all stems and a 2.6% increase for dicotyledons alone; (5) a change in species composition with the loss of pioneers, decrease in secondary species, and increase in the dominance of climax trees; (6) a decline in species richness from 88 to 83 species for the entire forest; (7) a decrease in diameter increment from 0.14 cm/yr in the years between 1946-51 to 0.09 cm/yr in the years between 1976-81 for all surviving stems; (8) an increase in standing stemwood and branch volume from 217 to 254 m^3/ha, with a net growth of 1.06 m^3/ha/yr; and (9) an increase in aboveground woody biomass from 122 to 145 t/ha with a net growth of 0.67 t/ha/yr. Patterns of disturbance and recovery appear to vary along elevational and topographic gradients within the Luquillo Forest. Windthrow is more common at lower elevations where there are large trees in valleys; breakage is more prevalent on slopes and ridges at higher elevations. In the Colorado Forest, biomass recovery appears linear. In the Tabonuco Forest below it, recovery is along a convex curve. In the Dwarf Forest at the summits, it may also be linear, but slower than in the Colorado Forest.

Wen, S.; Fetcher, N.; Zimmerman, J.K. 2008. Acclimation of tropical tree species to hurricane disturbance: Ontogenetic differences. Tree Physiology. 28: 935-946. https://doi.org/10.1093/treephys/28.6.935

We investigated acclimation responses of seedlings and saplings of the pioneer species *Cecropia schreberiana* Miq. and three non-pioneer species, *Dacryodes excelsa* Vahl, *Prestoea acuminata* (Willdenow) H.E. Moore var. *montana* (Graham) Henderson and Galeano, and *Sloanea berteriana* Choisy ex DC, following a hurricane disturbance in a lower montane wet forest in Puerto Rico. Measurements were made, shortly after passage of the hurricane, on leaves expanded before the hurricane (pre-hurricane leaves) and, at a later time, on recently matured leaves that developed after the hurricane (post-hurricane leaves) from both seedlings and saplings at sites that were severely damaged by the hurricane (disturbed sites) and at sites with little disturbance (undisturbed sites). Pre-hurricane leaves of the non-pioneer species had relatively low light-saturated photosynthetic rates (A_{max}) and stomatal conductance (g_s); neither A_{max} nor g_s responded greatly to the increase in irradiance that resulted from the disturbance, and there were few significant differences between seedlings and saplings. Pre-hurricane leaves of plants at undisturbed sites had low dark respiration rates per unit area (R_d) and light compensation points (LCP), whereas pre-hurricane leaves of plants at disturbed sites had significantly higher R_d and LCP. Post-hurricane leaves of plants at disturbed sites had significantly higher A_{max} and R_d than plants at undisturbed sites. Compared with seedlings, saplings had higher A_{max} and R_d and showed greater acclimation to the increase in irradiance that followed the disturbance. Post-hurricane leaves of the non-pioneer species had

significantly lower Amax and were less responsive to changes in irradiance than the pioneer species C. schreberiana. Variation in A_{max} across light environments and stages was strongly related to differences in leaf mass per unit area (LMA), especially in the non-pioneer species. As indicated by V_{cmax} or J_{max} per unit nitrogen, light acclimation of A_{max} was determined by leaf morphology (LMA) for the non-pioneer species and by both leaf morphology and leaf biochemistry for *C. schreberiana*. Ontogenetic changes in A_{max} were attributable to changes in leaf morphology. The ontogenetic component of variation in A_{max} across light environments and stages differed among species, ranging from 36 to 59% for the non-pioneer species (*D. excelsa*, 59.3%; *P. acuminata* var. montana, 44.7%; and *S. berteriana*, 36.3%) compared with only 17% in the pioneer species *C. schreberiana*.

Willig, M.R.; Bloch, C.P.; Brokaw, N. [and others]. 2007. Cross-Scale Responses of Biodiversity to Hurricane and Anthropogenic Disturbance in a Tropical Forest. Ecosystems. 10(5): 824-838. https://doi.org/10.1007/s10021-007-9054-7

In studies of biodiversity, considerations of scale—the spatial or temporal domain to which data provide inference—are important because of the non-arithmetic manner in which species richness increases with area (and total abundance) and because fine-scale mechanisms (for example, recruitment, growth, and mortality of species) can interact with broad scale patterns (for example, habitat patch configuration) to influence dynamics in space and time. The key to understanding these dynamics is to consider patterns of environmental heterogeneity, including patterns produced by natural and anthropogenic disturbance. We studied how spatial variation in three aspects of biodiversity of terrestrial gastropods (species richness, species diversity, and nestedness) on the 16-ha Luquillo Forest Dynamics Plot (LFDP) in a tropical forest of Puerto Rico was affected by disturbance caused by Hurricanes Hugo and Georges, as well as by patterns of historic land use. Hurricane-induced changes in spatial organization of species richness differed from those for species diversity. The gamma components of species richness changed after the hurricanes and were significantly different between Hurricanes Hugo and Georges. Alpha and two beta components of species richness, one related to turnover among sites within areas of similar land use and one related to variation among areas of different land use, varied randomly over time after both hurricanes. In contrast, gamma components of species diversity decreased in indistinguishable manners after both hurricanes, whereas the rates of change in the alpha component of species diversity differed between hurricanes. Beta components of diversity related to turnover among sites declined after both hurricanes in a consistent fashion. Those related to turnover among areas with different historic land uses varied stochastically. The immediate effect of hurricanes was to reduce nestedness of gastropod assemblages. Thereafter, nestedness increased during post-hurricane secondary succession, and did so in the same way, regardless of patterns of

historic land use. The rates of change in degree of nestedness during secondary succession were different after each hurricane as a result of differences in the severity and extent of the hurricane-induced damage. Our analyses quantified temporal changes in the spatial organization of biodiversity of gastropod assemblages during forest recovery from hurricane-induced damage in areas that had experienced different patterns of historic human land use, and documented the dependence of biodiversity on spatial scale. We hypothesize that cross-scale interactions, likely those between the local demographics of species at the fine scale and the landscape configuration of patches at the broad scale, play a dominant role in affecting critical transfer processes, such as dispersal, and its interrelationship with aspects of biodiversity. Cross-scale interactions have significant implications for the conservation of biodiversity, as the greatest threats to biodiversity arise from habitat modification and fragmentation associated with disturbance arising from human activities.

Willig, M.R.; Bloch, C.P.; Presley, S.J. 2014. Experimental decoupling of canopy opening and debris addition on tropical gastropod populations and communities. Forest Ecology and Management. 332: 103-117.
https://doi.org/10.1016/j.foreco.2014.01.036
Download: https://www.fs.usda.gov/treesearch/pubs/49016

Climate-induced disturbances such as hurricanes affect the structure and functioning of many ecosystems, especially those in the Caribbean Basin, where effects are well documented with regard to biodiversity and biogeochemical dynamics. Because climate change will likely alter the frequency or intensity of such storms, it is increasingly important to understand the mechanistic bases for ecosystem responses. However, this is particularly difficult to do in the absence of manipulative experiments that decouple confounded factors such as canopy opening and debris deposition. To address this issue, we exploited a replicated factorial design to experimentally distinguish the effects of canopy opening and debris deposition on population- and community-level characteristics of gastropods in the Luquillo Experimental Forest of Puerto Rico. Despite considerable spatial variation, abundances of all gastropods (combined) as well as abundances of each of 3 species (i.e., *Alcadia striata*, *Platysuccinea portoricensis*, and *Polydontes acutangula*) responded significantly to canopy opening while abundances of each of 2 species (i.e., *Pl. portoricensis*, and *Po. acutangula*) responded significantly to debris deposition within two years of experimental manipulation. In contrast, two species (i.e., *Gaeotis nigrolineata* and *Nenia tridens*) did not respond to any experimental manipulations in the short term. Moreover, species composition did not differ between pre- and post-manipulation periods, in part because of considerable variation among replicated blocks. In contrast, canopy removal consistently affected species richness, Shannon diversity, and rarity, while debris deposition consistently affected species richness and Shannon

diversity. Neither treatment affected species dominance or evenness. Longer-term responses of the gastropod fauna were more complex. Although considerable interspecific heterogeneity characterized responses of the gastropod fauna, temporal variation in mean abundance for each of the three manipulative treatments was similar to that of the non-manipulated treatment when abundances were combined for all species. In contrast, temporal variation in each of the manipulative treatments was unrelated to temporal variation in the non-manipulated treatment for species richness, evenness, dominance, and rarity. Moreover, temporal variation in abundance generally differed between at least two of the manipulative treatments for most species and temporal variation in components of taxonomic biodiversity generally differed between manipulative treatments as well. Temporal variation in species composition was considerable and comparable for each of the four treatment combinations. Species composition within each treatment combination varied over time in ways unrelated to temporal variation in the other treatment combinations, including the reference treatment (i.e., no canopy trimming and no debris addition). Manipulated treatments were surrounded by large areas of intact forest, and tabonuco forest generally exhibits appreciable spatial and temporal variation. Natural spatiotemporal variation in the study system likely overwhelmed many of the effects of experimental manipulations on gastropod populations or communities via edge effects and recruitment of individuals from nearby less disturbed portions of the landscape.

Willig, M.R.; Camilo, G.R. 1991. The Effect of Hurricane Hugo on Six Invertebrate Species in the Luquillo Experimental Forest of Puerto Rico. Biotropica. 23(4a): 455-461. https://doi.org/10.2307/2388266

Although the importance of disturbance regimes in affecting ecosystem structure and function is becoming an accepted paradigm in ecology, the consequences of catastrophic events are poorly understood. On 18 September 1989 Hurricane Hugo struck Puerto Rico, with the center of the hurricane passing within ten kilometers of the Luquillo Experimental Forest. This provided a rare opportunity to document direct and indirect effects of a natural disturbance of high intensity, large scale, but low frequency on selected aspects of animal ecology The densities and spatial distributions of six species of common invertebrates (four snails, *Caracolus caracolla*, *Polydontes acutangula*, *Nenia tridens*, and *Gaeotis nigrolineata*, and two walking sticks, *Lamponius portoricensis* and *Agamemnon iphimedeia*) in the tabonuco rain forest were estimated before and after the hurricane. Circular quadrats (radius = 5 m; area = 78.54 m2) were established at each of 40 points in the Bisley watersheds. Numbers of individuals of each species were counted during nighttime surveys and densities were compared before and after the hurricane via paired t-tests. Both species of walking stick and three of the four species of snail exhibited statistically significant reductions in density

after the hurricane. Densities of *N. tridens*, *G. nigrolineata*, and *A. iphimedeia* were reduced to the point that no specimens were detected in posthurricane surveys. In fact, all species of invertebrates were so rare after the hurricane that comparisons of spatial distribution were only possible for *C. caracolla*, and its distribution was significantly less clumped after Hurricane Hugo (G-test). At the Bisley watersheds, all size categories of *C. caracolla* suffered similar reductions in density; no significant alteration in size distribution was detected after the hurricane (G-test).

Willig, M.R.; Moorhead, D.L.; Cox, S.B. [and other]. 1996. Functional Diversity of Soil Bacterial Communities in the Tabonuco Forest: Interaction of Anthropogenic and Natural Disturbance. Biotropica. 28(4a): 471-483. https://doi.org/10.2307/2389089

Anthropogenic and natural disturbances plav critical roles in affecting the structure and function of Caribbean ecosystems, where hurricanes represent important disturbances superimposed on a landscape modified by human agricultural and forestry practices. Based on the differential catabolism of a suite of 128 carbon sources by soil bacterial communities, we focus on four aspects of functional diversity (total substrate activity, substrate richness, substrate evenness, substrate diversity) in the tabonuco forest of Puerto Rico, and assess the degree to which their spatial variability is a consequence of historical landuse or impacts of Hurricane Hugo. Considerable microspatial heterogeneity characterizes the functional diversity of forest soil communities, but the degree of hurricane damage to aboveground plant communities is positively related to all four indexes of functional diversity 5yr after the hurricane. No differences in functional diversity were detected with respect to historical landuse, after controlling for the effects of hurricane damage. However, this lack of significance may be an artifact because the spatial distribution of hurricane damage is not independent of historical landuse. As a consequence, contemporary studies of spatial heterogeneity that do not account for historical patterns of anthropogenic or natural disturbance may yield spurious or incorrect conclusions. Long-term studies help to rectify this problem and are especially important within the context of evaluating the impacts of increasing human demands on natural ecosystems.

Willig, M.R.; Presley, S.J. 2022. Long-term spatiotemporal variation in density of a tropical folivore: responses to a complex disturbance regime. Oecologia. 199: 979-994. https://doi.org/10.1007/s00442-022-05227-3

The Anthropocene is a time of unprecedented and accelerating rates of environmental change that includes press (e.g., climate change) and pulse disturbances (e.g., cyclonic storms, land use change) that interact to affect spatiotemporal dynamics in the density, distribution, and

biodiversity of organisms. We leverage three decades of spatially explicit data on the density of a tropical folivore (*Lamponius portoricensis* [Insecta, Phasmida]) in a hurricane-mediated ecosystem (montane rainforest of Puerto Rico), along with associated environmental attributes, to disentangle the effects of interacting disturbances at multiple spatial scales. Spatiotemporal variation in density at a small spatial scale is affected by disturbance-related characteristics (hurricane severity, time after most recent major hurricane, ambient temperature, and understory temperature), legacies of previous land use, and understory habitat structure. Nonetheless, only a small proportion of spatiotemporal variation in density was related to those characteristics. In contrast, the majority of interannual variation in mean density at a larger scale was related to disturbance characteristics and understory habitat structure. These factors combine to affect a weak and declining trend in the density of *L. portoricensis* over time. The low resistance of L. portoricensis to Hurricane Hugo, as compared to Hurricanes Georges and Maria, likely arose because a drought followed Hurricane Hugo. The disturbance regime of the region is predicted to include increases in ambient temperatures, frequency of high-intensity storms, and frequency of droughts. Such trends may combine to threaten the conservation status of *L. portoricensis*, and other species with which it shares similar life history characteristics.

Willig, M.R.; Presley, S.J. 2022. Long-term trends in gastropod abundance and biodiversity: Disentangling effects of press versus pulse disturbances. Global Ecology and Biogeography. 31(2): 247-265. https://doi.org/10.1111/geb.13425

Aim: Climate-induced pulse (e.g., hurricanes) and press (e.g., global warming) disturbances represent threats to populations, communities, and the ecosystem services that they provide. We leveraged three decades of annual data on tropical gastropods to quantify the effects of major hurricanes, associated secondary succession, and global warming on abundance, biodiversity, and species composition. Location: Luquillo Mountains, Puerto Rico. Methods: Gastropod abundance, biodiversity, and composition were estimated annually for each of 27 years in a tropical montane forest that experienced three major hurricanes (Hugo, Georges, and Maria). Generalized linear mixed-effects, linear mixed-effects, and linear models evaluated population- and community-level responses to year, ambient temperature, understorey temperature, hurricane, and time since hurricane. Variation partitioning determined the unique and shared variation in biotic responses associated with temperature, disturbance, and succession. Results: Rather than declining, gastropod abundances generally increased through time, whereas the responses of biodiversity were weak and scale dependent. Hurricanes and associated secondary succession, rather than ambient atmospheric temperature, moulded long-term trends in abundances and biodiversity. Main conclusions: Global warming over the past 30 years has not progressed sufficiently to elicit

significant responses by gastropods in the Luquillo Mountains. Rather, effects from pulse disturbances (i.e., hurricanes) and secondary succession currently drive long-term variation in abundance and biodiversity. Gastropods evince high resilience in this tropical ecosystem. Historical exposure to recurrent hurricanes likely imbued the fauna with broad niches that make them resistant to current levels of global warming. We predict that biotic resiliency will be challenged once changes in temperature exceed interannual and inter-habitat differences that typify this hurricane-mediated system, or combine with an increased frequency of hurricanes and droughts to alter associations among environmental characteristics that define the fundamental niches of species. Only then might significant declines in abundance or the appearance of novel communities characterize the gastropod fauna in the Luquillo Mountains.

Willig, M.R.; Presley, S.J.; Bloch, C.P. 2011. Long-term dynamics of tropical walking sticks in response to multiple large-scale and intense disturbances. Oecologia. 165(2): 357-368. https://doi.org/10.1007/s00442-010-1737-7

Understanding the effects of disturbance and secondary succession on spatio-temporal patterns in the abundance of species is stymied by a lack of long-term demographic data, especially in response to infrequent and high intensity disturbances, such as hurricanes. Moreover, resistance and resilience to hurricane-induced disturbance may be mediated by legacies of previous land use, although such interactive effects are poorly understood, especially in tropical environments. We address these central issues in disturbance ecology by analyzing an extensive dataset, spanning the impacts of Hurricanes Hugo and Georges, on the abundance of a Neotropical walking stick, *Lamponius portoricensis*, in tabonuco rainforest of Puerto Rico during the wet and dry seasons from 1991 to 2007. By synthesizing data from two proximate sites in tabonuco forest, we show that resistance to Hurricane Hugo (97% reduction in abundance) was much less than resistance to Hurricane Georges (21% reduction in abundance). Based on a powerful statistical approach (generalized linear mixed-effects models with Poisson error terms), we documented that the temporal trajectories of abundance during secondary succession (i.e., patterns of resilience) differed between hurricanes and among historical land use categories, but that the effects of hurricanes and land use histories were independent of each other. These complex results likely arise because of differences in the intensities of the two hurricanes with respect to microclimatic effects (temperature and moisture) in the forest understory, as well as to time-lags in the response of *L. portoricensis* to changes in the abundance and distribution of preferred food plants (*Piper*) in post-hurricane environments.

Willig, M.R.; Presley, S.J.; Cullerton, E.I. 2021. A canonical metacommunity structure over 3 decades: Ecologically consistent but spatially dynamic patterns in a hurricane-prone montane forest. Oecologia. 196: 919-933. https://doi.org/10.1007/s00442-021-04968-x

The Anthropocene is a time of rapid change induced by human activities, including pulse and press disturbances that affect the species composition of local communities and connectivity among them, giving rise to spatiotemporal dynamics at multiple scales. We evaluate effects of global warming and repeated intense hurricanes on gastropod metacommunities in montane tropical rainforests of Puerto Rico for each of 28 consecutive years. Specifically, we quantified metacommunity structure each year; assessed effects of global warming, hurricane-induced disturbance, and secondary succession on interannual variation in metacommunity structure; and evaluated legacies of previous land use on metacommunity structure. Gastropods were sampled annually during a 28-year period characterized by disturbance and succession associated with 3 major hurricanes (Hurricanes Hugo, Georges, and Maria). For each year, we evaluated coherence (the extent to which the environmental distributions of species are uninterrupted along a common latent environmental gradient), species range turnover, and species range boundary clumping; and conducted co-occurrence analyses for each pair of species. We used generalized linear mixed-effects model to evaluate long-term responses of the metacommunity to aspects of global warming and disturbance. Metacommunity structure was remarkably stable, with consistent patterns of species co-occurrence. Disturbance, warming, and successional stage had little effect on metacommunity structure. Despite great temporal variation in environmental conditions, groups of species tracked their niche through space and time to maintain the same general structure. Consequently, metacommunity structure was highly resistant and resilient to multiple disturbances, even those that greatly altered forest structure.

Wohl, E.; Hinshaw, S.K.; Scamardo, J.E. [and other]. 2018. Transient organic jams in Puerto Rican mountain streams after hurricanes. River Research and Applications. 35(3): 280-289. https://doi.org/10.1002/rra.3405

Extreme storms in forested environments commonly increase inputs of coarse particulate organic matter (CPOM) and large wood (LW) to streams. Protruding boulders and bedforms, mid-channel bars, and standing trees can trap CPOM and LW. These organic accumulations can become large enough to span the bankfull channel width, or the accumulations can be predominantly along the channel margins. We refer to both types of accumulations as transient organic jams (TOJs). TOJs can create diverse geomorphic and ecological effects in channel and floodplain environments. We use data collected from mountain streams of the Luquillo Mountains of north-eastern Puerto Rico following September 2017 Hurricanes

Irma and Maria. We examine the location, characteristics, and geomorphic effects of TOJs in channel segments representing diverse drainage areas and channel gradients. We ask three questions: (a) Does the downstream spacing of TOJs correlate with variables such as drainage area or channel gradient? (b) What variables best predict the volume of organic matter within individual TOJs or within a channel segment? And (c) is there a threshold within a river network that separates channel segments with channel-spanning versus marginal TOJs? Datasets include multiple TOJs along each of 12 stream segments and presence/absence of channel-spanning TOJs along an additional six streams. Data analysis with multiple linear regressions indicates that downstream spacing, average volume, and total volume per channel length of TOJs correlate significantly with bankfull channel width. Using the akaike information criterion with correction (AICc) model selection method, Strahler stream order has the most influence on the probability of TOJs being marginal or spanning.

Woolbright, L.L. 1991. The Impact of Hurricane Hugo on Forest Frogs in Puerto Rico. Biotropica. 23(4a): 462-467. https://doi.org/10.2307/2388267

Hurricane Hugo caused extensive damage to the Luquillo Experimental Forest in September 1989 Individually marked *Eleutherodactylus* coqui were monitored in two study plots from January 1987 through October 1990. Survivorship estimates of adults for the period including the storm were within the normal range from previous years. Juveniles suffered severe reductions, primarily among the smaller size classes. By October 1990 adult population density had increased fourfold over prehurricane levels, although adults were smaller. Juvenile numbers also appeared to be increasing, but had not yet reached prehurricane densities. The rapid increase in density may have resulted from an increase in retreat sites and a decrease in invertebrate predators. Auditory censuses suggested that density changes for other species ranged from a 14 percent increase for the relatively common *E. hedricki* to an 83 percent decrease for the relatively rare *E. richmondi*.

Woolbright, L.L. 1996. Disturbance Influences Long-Term Population Patterns in the Puerto Rican Frog, *Eleutherodactylus* coqui (Anura: Leptodactylidae). Biotropica. 28(4a): 493-501. https://doi.org/10.2307/2389091

Population estimates from 1987 to 1995 are reported for the terrestrial anuran, *Eleutherodactylus* coqui, from four long-term study plots in the Luquillo Experimental Forest of northeastern Puerto Rico. The major factor influencing population size during this time was Hurricane Hugo, which deposited much of the canopy onto the forest floor in 1989. This increase in ground-level structure was in part responsible for a six-fold increase in the number of adult frogs in 1990 and a large increase in the number of juvenile frogs in

1991. Population densities since Hurricane Hugo have been influenced by succession, with continued high densities associated with thickets of Cecropia and Heliconia. Treefalls, which are similar to hurricanes on a local scale, also were shown to influence population sizes. Years with prolonged dry periods reduced numbers of juvenile frogs, but rainfall patterns alone did not explain most population variation. Population levels of invertebrate predators were related to variation in frog numbers.

Woolbright, L.L.; Stewart, M.M. 2008. Spatial and Temporal Variation in Color Pattern Morphology in the Tropical Frog, *Eleutherodactylus coqui*. Copeia. 2: 431-437. https://doi.org/10.1643/CG-06-092

We recorded the pattern morph for 9,950 frogs captured at nine locations in northeastern Puerto Rico over a 25-year period from 1978–2002. Data revealed 21 distinct pattern morphs including a variety of stripes, bars, and spots. Analysis of morph frequencies among plots showed significant differences, with longitudinal stripes more common in grassland and disturbed areas, and spot and bar morphs more common in forests where palm and bromeliad axils are important habitat features. Comparison of morph frequencies through time at the same sites showed temporal shifts immediately following Hurricane Hugo in 1989. We suggest that the pattern polymorphism is maintained in part by local habitat matching resulting from selection pressure from visual predators.

Worthy, S.J.; Rubio, V.E.; Staiger, K. [and others]. 2021. Site-specific impacts of a major hurricane on alpha and beta diversity in tropical forest seedling communities. Ecosphere. 12(7): e03651. https://doi.org/10.1002/ecs2.3651
Download: https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.3651

Large scale disturbances are known to impact the alpha and beta diversity of communities. However, whether these disturbances increase or decrease diversity is often debated. The goal of this study was to quantify how the diversity of the seedling community was impacted within and across elevation in the El Yunque forest of Puerto Rico following a major hurricane. We tested two alternative hypotheses, that hurricanes are relatively more homogenizing or non-homogenizing forces, by quantifying changes in alpha and beta diversity of the seedling community post-hurricane. This approach highlights whether ecological mechanisms associated with community homogenization (species-specific survival, successional processes, and reduced environmental heterogeneity) or non-homogenization (resource release, increased environmental heterogeneity, and stochastic processes) structure the seedling community post-hurricane. We compared species richness, Fisher's α, Simpson's evenness, and multiple aspects of beta diversity within and among 25 seedling plots at

300, 400, and 500 m in elevation pre- and post-hurricane. We found that species richness, diversity, and evenness were higher post-hurricane, but abundance decreased 19%. Increases in alpha diversity suggest that hurricanes are non-homogenizing forces potentially linked with increases in light levels promoting colonization of early-successional species and resource release for other light-demanding species. The beta diversity results varied in their support for hurricanes as homogenizing depending upon the spatial scale of the analysis, potentially due to a combination of mechanisms including species-specific survival and site-specific differences. To fully grasp how the seedling community responds and recovers from disturbance, additional long-term monitoring will be needed to allow insight into the future of species richness, abundance, and spatial and temporal changes in community composition.

Wunderle, J.M. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: The first 18 months. Condor. 97: 879-896.
https://doi.org/10.2307/1369528
Download: https://www.fs.usda.gov/research/treesearch/66377

Bird populations in a subtropical wet forest were monitored every two to three weeks with mist nets and point counts beginning two weeks after the passage of Hurricane Hugo in September 1989. The results were compared with those of a pre-hurricane study in the same locations in which birds were sampled in forest understory and openings. Capture rates were initially higher than in the previous study, due to displaced canopy dwellers foraging in the understory. The shift of canopy dwellers may have obscured expected declines in nectarivores and fruit/seedeaters and contributed to increased detections of omnivores and insectivores. Bird captures and fruit production peaked 93–156 days after the storm in pre-existing gaps, where higher capture rates and a distinct assemblage of birds occurred in contrast to sites without fruit (forest understory and a powerline opening). Captures in pre-existing gaps decreased as fruit production ceased, and overall captures declined to baseline levels after 198 days. After one year of recovery, new gaps and forest understory became distinguishable on the basis of their unique foliage profiles. Although different bird assemblages had been found in forest understory and in gaps prior to the hurricane, these assemblages lost their distinctiveness after the storm. It may take many years after a hurricane for forest understory and gaps to become sufficiently distinct in structure and resources before birds differentiate between the two habitats.

Wunderle, J.M. 1999. Pre- and Post-Hurricane Fruit Availability: Implications for Puerto Rican Parrots in the Luquillo Mountains. Caribbean Journal of Science. 35(3-4): 249-264.
Download: https://www.fs.usda.gov/treesearch/pubs/30302

Fruit availability on 25 plant species, consumed or potentially consumed by the Puerto Rican Parrot (*Amazona vittata*), was studied to document the seasonal and annual variation in fruit production in the Luquillo Mountains. In the 33 months before Hurricane Hugo, an annual cycle in the number of species with ripe fruit was evident, with a peak in October-February and a trough during June-July. About half the plant species showed this annual fruiting cycle. Irregular noncyclic fruiting was found in the other half, and varied among species in annual duration. Fruit production reached its lowest point in October 1989, just after Hurricane Hugo, when 72% of the broadleaf foliage was lost and only one species had ripe fruit. The number of fruiting species subsequently increased, but the cyclic fruiting pattern, evident in the number of fruiting species before the storm, disappeared and was not observed during 27 months after the storm. This noncyclic pattern was attributed mostly to species with annual fruiting cycles in which annual fruiting shifted out of phase, was suppressed after the hurricane, or both. Parrot breeding was associated with fruiting, as breeding occurred during fruiting peaks before the storm, and was delayed in the first season after the storm, but returned to normal by the second season. Thus parrots faced considerable annual and year-to-year variation in fruit availability prior to the hurricane, and substantial fruit loss afterwards, followed by a recovery involving changes in fruiting phenology of individual species and the overall community.

Wunderle, J.M.; Mercado, J.E.; Parresol, B.; Terranova, E. 2004. Spatial Ecology of Puerto Rican Boas (*Epicrates inornatus*) in a Hurricane Impacted Forest. Biotropica. 36(4): 555-571. https://doi.org/10.1111/j.1744-7429.2004.tb00350.x
Download: https://www.fs.usda.gov/treesearch/pubs/26045

Spatial ecology of Puerto Rican boas (*Epicrates inornatus*, Boidae) was studied with radiotelemetry in a subtropical wet forest recovering from a major hurricane (7–9 yr previous) when Hurricane Georges struck. Different boas were studied during three periods relative to Hurricane Georges: before only; before and after; and after only. Mean daily movement per month increased throughout the three periods, indicating that the boas moved more after the storm than before. Radio-tagged boas also became more visible to observers after the hurricane. Throughout the three periods, the sexes differed in movements, with males moving greater distances per move and moving more frequently than females. Males showed a bimodal peak of movement during April and June in contrast to the females' July peak. Sexes did not differ in annual home range size, which had a median value of 8.5 ha (range = 2.0–105.5 ha, $N = 18$) for 95 percent adaptive kernal. Females spent more time on or below ground than did males, which were mostly arboreal. Trees used by boas had larger diameters and more vines than random trees. Hurricane winds that strip leaves, vines, and branches from trees may reduce cover for boas and limit access to arboreal sites, at least for several

years until succession brings about recovery with increased vine growth. Boas were especially difficult to observe; telemetrically monitored boas were detected visually at an average of only 15 percent of their fix sites, indicating that the species is more abundant than generally perceived.

Wymore, A.S.; León, M.C.; Shanley, J.B. [and other]. 2019. Hysteretic Response of Solutes and Turbidity at the Event Scale Across Forested Tropical Montane Watersheds. Frontiers in Earth Science. 7: 126.
https://doi.org/10.3389/feart.2019.00126
Download: https://www.frontiersin.org/articles/10.3389/feart.2019.00126/full

Concentration-discharge relationships are a key tool for understanding the sources and transport of material from watersheds to fluvial networks. Storm events in particular provide insight into variability in the sources of solutes and sediment within watersheds, and the hydrologic pathways that connect hillslope to stream channel. Here we examine high-frequency sensor-based specific conductance and turbidity data from multiple storm events across two watersheds (Quebrada Sonadora and Rio Icacos) with different lithology in the Luquillo Mountains of Puerto Rico, a forested tropical ecosystem. Our analyses include Hurricane Maria, a category 5 hurricane. To analyze hysteresis, we used a recently developed set of metrics to describe and quantify storm events including the hysteresis index (HI), which describes the directionality of hysteresis loops, and the flushing index (FI), which can be used to infer whether the mobilization of material is source or transport limited. We also examine the role of antecedent discharge to predict hysteretic behavior during storms. Overall, specific conductance and turbidity showed contrasting responses to storms. The hysteretic behavior of specific conductance was similar across sites, displaying clockwise hysteresis and a negative FI indicating proximal sources of solutes and consistent source limitation. In contrast, the directionality of turbidity hysteresis was significantly different between watersheds, although both had strong flushing behavior indicative of transport limitation. Overall, models that included antecedent discharge did not perform any better than models with peak discharge alone, suggesting that the magnitude and trajectory of an individual event was the strongest driver of material flux and hysteretic behavior. Hurricane Maria produced unique hysteresis metrics within both watersheds, indicating a distinctive response to this major hydrological event. The similarity in response of specific conductance to storms suggests that solute sources and pathways are similar in the two watersheds. The divergence in behavior for turbidity suggests that sources and pathways of particulate matter vary between the two watersheds. The use of high-frequency sensor data allows the quantification of storm events while index-based metrics of hysteresis allow for the direct comparison of complex storm events across a heterogeneous landscape and variable flow conditions.

Yaffar, D.; Wood, T.E.; Reed, S.C. [and others]. 2021. Experimental warming and its legacy effects on root dynamics following two hurricane disturbances in a wet tropical forest. Global Change Biology. 27(24): 6423-6435. https://doi.org/10.1111/gcb.15870
Download: https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15870

Tropical forests are expected to experience unprecedented warming and increases in hurricane disturbances in the coming decades; yet, our understanding of how these productive systems, especially their belowground component, will respond to the combined effects of varied environmental changes remains empirically limited. Here we evaluated the responses of root dynamics (production, mortality, and biomass) to soil and understory warming (+4°C) and after two consecutive tropical hurricanes in our in situ warming experiment in a tropical forest of Puerto Rico: Tropical Responses to Altered Climate Experiment (TRACE). We collected minirhizotron images from three warmed plots and three control plots of 12 m^2. Following Hurricanes Irma and María in September 2017, the infrared heater warming treatment was suspended for repairs, which allowed us to explore potential legacy effects of prior warming on forest recovery. We found that warming significantly reduced root production and root biomass over time. Following hurricane disturbance, both root biomass and production increased substantially across all plots; the root biomass increased 2.8-fold in controls but only 1.6-fold in previously warmed plots. This pattern held true for both herbaceous and woody roots, suggesting that the consistent antecedent warming conditions reduced root capacity to recover following hurricane disturbance. Root production and mortality were both related to soil ammonium nitrogen and microbial biomass nitrogen before and after the hurricanes. This experiment has provided an unprecedented look at the complex interactive effects of disturbance and climate change on the root component of a tropical forested ecosystem. A decrease in root production in a warmer world and slower root recovery after a major hurricane disturbance, as observed here, are likely to have longer-term consequences for tropical forest responses to future global change.

You, C.; Petty, W.H. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a Primary Tree Species in the Luquillo Experimental Forest of Puerto Rico. Biotropica. 23(4a): 400-406. https://doi.org/10.2307/2388258

Changes in the population structure and recruitment characteristics of *Manilkara bidentata* populations were investigated at two sites (El Verde & Bisley) in the Luquillo Experimental Forest (LEF), at one month and nine months after Hurricane Hugo. Fatal damage occurred to 4 percent of the trees at the El Verde site. Severe damage to mature trees disrupted seed production. Sixty percent of the young seedling population was destroyed, mainly as a

result of burial by litter. For surviving seedlings, the posthurricane growth rate (in height) of old seedlings was 2 cm/mo, 17 times greater than that under prehurricane conditions. The prehurricane population of young seedlings had a large number of individuals and a long transition period (over 14 yr); whereas, the posthurricane population had fewer individuals and a shorter transition period (less than 2 yr). Increased growth rates of seedlings were related to increased light at the forest floor. The recruitment rate of the *Manilkara* population from the seedling size class into the sapling size class was greater than that under prehurricane conditions. Rapid adjustment to posthurricane conditions, high tree survival, and increased number of seedlings recruited into larger size classes may increase the abundance of Manilkara trees in the forest. These adaptations are especially significant in the LEF and other forests which experience frequent hurricane disturbances. Based upon the effects of Hurricane Hugo, it appears that hurricanes play an important role in releasing suppressed seedling growth of Manilkara populations and that hurricanes may contribute to the abundance of *Manilkara* trees in the LEF.

Zambrano, J.; Arellano, G; Swenson, N.G. [and others]. 2022. Analyses of three-dimensional species associations reveal departures from neutrality in a tropical forest. Ecology. 103: e3681. https://doi.org/10.1002/ecy.3681

The study of community spatial structure is central to understanding diversity patterns over space and species co-occurrence at local scales. Although most analytical approaches consider horizontal and vertical dimensions separately, in this study we introduce a three-dimensional spatial analysis that simultaneously includes horizontal and vertical species associations. Using tree census data (2000–2016) and allometries from the Luquillo forest plot in Puerto Rico, we show that spatial organization becomes less random over time as the forest recovered from land-use legacy effects and hurricane disturbance. Tree species vertical segregation is predominant in the forest with almost all species that co-occur in the horizontal plane avoiding each other in the vertical dimension. Horizontal segregation is less common than vertical, whereas three-dimensional aggregation (a proxy for direct tree competition) is the least frequent type of spatial association. Furthermore, dominant species are involved in more non-random spatial associations, implying that species co-occurrence is facilitated by species segregation in space. This novel three-dimensional analysis allowed us to identify and quantify tree species spatial distributions, how interspecific competition was reduced through forest structure, and how it changed over time after disturbance, in ways not detectable from two-dimensional analyses alone.

Zhang, J.; Bras, R.L.; Longo, M. [and other]. 2022. Future Hurricanes Will Increase Palm Abundance and Decrease Aboveground Biomass in a Tropical Forest. Geophysical Research Letters. 49(19): e2022GL100090. https://doi.org/10.1029/2022GL100090
Download: https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2022GL100090

Hurricanes are expected to intensify throughout the 21st century, yet the impact of frequent major hurricanes on tropical ecosystems remains unknown. To investigate tropical forest damage and recovery under different hurricane regimes, we generate a suite of scenarios based on Coupled Model Intercomparison Project Phase 6 climate projections and increased hurricane recurrence and intensity for the Luquillo Experimental Forest, Puerto Rico. We then use the Ecosystem Demography model to predict changes in carbon stocks, forest structure and composition. Our results indicate that frequent hurricane disturbances in the future would decrease the overall aboveground biomass, decrease the dominance of late-successional species, but increase the dominance of palm species. Warmer climates with increased CO_2 would have little effect on the functional-type composition but increase the aboveground biomass. However, the predicted climate and CO_2 fertilization effects would not compensate for the biomass loss due to more frequent severe-hurricane disturbances.

Zhang, J.; Bras, R.L.; Longo, M. [and other]. 2022. The impact of hurricane disturbances on a tropical forest: implementing a palm plant functional type and hurricane disturbance module in ED2-HuDi V1.0. Geoscientific Model Development. 15: 5107-5126. https://doi.org/10.5194/gmd-15-5107-2022
Download: https://www.fs.usda.gov/treesearch/pubs/64487

Hurricanes commonly disturb and damage tropical forests. Hurricane frequency and intensity are predicted to change under the changing climate. The short-term impacts of hurricane disturbances to tropical forests have been widely studied, but the long-term impacts are rarely investigated. Modeling is critical to investigate the potential response of forests to future disturbances, particularly if the nature of the disturbances is changing with climate. Unfortunately, existing models of forest dynamics are not presently able to account for hurricane disturbances. Therefore, we implement the Hurricane Disturbance in the Ecosystem Demography model (ED2) (ED2-HuDi). The hurricane disturbance includes hurricane-induced immediate mortality and subsequent recovery modules. The parameterizations are based on observations at the Bisley Experimental Watersheds (BEW) in the Luquillo Experimental Forest in Puerto Rico. We add one new plant functional type (PFT) to the model – Palm, as palms cannot be categorized into one of the current existing PFTs and are known to be an abundant component of tropical forests worldwide. The model is calibrated with observations at BEW using the generalized likelihood uncertainty estimation

(GLUE) approach. The optimal simulation obtained from GLUE has a mean relative error of −21 %, −12 %, and −15 % for stem density, basal area, and aboveground biomass, respectively. The optimal simulation also agrees well with the observation in terms of PFT composition (+1 %, −8 %, −2 %, and +9 % differences in the percentages of "Early", "Mid", "Late", and "Palm" PFTs, respectively) and size structure of the forest (+0.8 % differences in the percentage of large stems). Lastly, using the optimal parameter set, we study the impact of forest initial condition on the recovery of the forest from a single hurricane disturbance. The results indicate that, compared to a no-hurricane scenario, a single hurricane disturbance has little impact on forest structure (+1 % change in the percentage of large stems) and composition (<1 % change in the percentage of each of the four PFTs) but leads to 5 % higher aboveground biomass after 80 years of succession. The assumption of a less severe hurricane disturbance leads to a 4 % increase in aboveground biomass.

Zhang, J.; Heartsill Scalley, T.; Bras, R.L. 2022. Forest Structure and Composition Are Critical to Hurricane Mortality. Forests. 13: 202. https://doi.org/10.3390/f13020202
Download: https://www.mdpi.com/1999-4907/13/2/202

Hurricanes can cause severe damage to tropical forests. To understand the nature of hurricane impacts, we analyze and compare immediate effects from category-4 hurricane María in 2017 and category-3 hurricane Hugo in 1989 at Bisley Experimental Watersheds (BEW) in the Luquillo Experimental Forest, Puerto Rico. We show that hurricane María caused lower mortality than hurricane Hugo, even though hurricane María was a stronger event with higher sustained wind. The lower mortality was due to the combination of lower accumulated cyclone energy at the site and more wind-resistant forest structure and composition at the time of disturbance. We compare our study site with a nearby location that has the same forest type, Luquillo Forest Dynamics Plot (LFDP), and describe the similarities and differences of mortality and impact factors between the two sites during the two events. During hurricane Hugo, LFDP experienced much lower mortality than BEW, even though the accumulated cyclone energy at LFDP was higher. The difference in mortality was due to contrasting forest structure and composition of the two sites. Our results demonstrate that forest structure and composition at the time of the disturbance were more critical to hurricane-induced mortality at the two sites than accumulated cyclone energy.

Zhang, J.; Heartsill Scalley, T.; Bras, R.L. 2022. Parsing Long-Term Tree Recruitment, Growth, and Mortality to Identify Hurricane Effects on Structural and Compositional Change in a Tropical Forest. Forests. 13: 796. https://doi.org/10.3390/f13050796
Download: https://www.mdpi.com/1999-4907/13/5/796

After hurricane disturbances in tropical forests, the size structure and species composition are affected by immediate mortality, and subsequent recruitment and individual growth. Often, immediate post-disturbance stand-level data are presented but understanding of the components that affect changes in growth and longer-term responses to forest structure and composition are lacking. To answer questions about how mortality, recruitment, and growth change among successional Plant Functional Types (PFT) through time after a hurricane disturbance, we use long-term census data (1989-2014) collected in the Luquillo Experimental Forest, Puerto Rico. We developed an algorithm to fill missing diameter data from the long-term data set that was collected three months after Hurricane Hugo; and subsequently at five-year intervals. Both the immediate hurricane-induced mortality and subsequent mortality were lower in stems with larger diameters, but varied among successional PFTs Early, Mid, Late, and Palm. Tree growth rates were observed to decrease with time since the hurricane disturbance. Five years after the hurricane, mortality was minimal but then increased gradually with time. In contrast, recruitment was highest five years after the hurricane and then decreased with time. The palm *Prestoea montana* became the most abundant species in the forest after the hurricane, as it had the lowest immediate hurricane-induced and subsequent mortality, and the highest recruitment. Twenty-five years after the hurricane, the palm and the Late PFT dominate the forest after shifting species composition from pre-hurricane conditions.

Zieminska, K.; Bibbo, S.; Farrar, S. [and others]. 2023. Shifts in wood anatomical traits after a major hurricane. Functional Ecology. 37: 3000-3014.
https://doi.org/10.1111/1365-2435.14451
Download: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.14451

Trait variation across individuals and species influences the resistance and resilience of ecosystems to disturbance, and the ability of individuals to capitalize on post-disturbance conditions. In trees, the anatomical structure of xylem directly affects plant function and, consequently, it is a valuable lens through which to understand resistance and resilience to disturbance. To determine how hurricanes affect wood anatomy of tropical trees, we characterized a set of anatomical traits in wood produced before and after a major hurricane for 65 individuals of 10 Puerto Rican tree species. We quantified variation at different scales (among and within species, and within individuals) and determined trait shifts between the pre- and post-hurricane periods. We also assessed correlations between traits and growth rates. While the majority of anatomical trait variation occurred among species, we also observed substantial variation within species and individuals. Within individuals, we found significant shifts for some traits that generally reflected increased hydraulic conductivity in the post-hurricane period. We found weak evidence for an association between individual

xylem anatomical traits and diameter growth rates. Ultimately, within-individual variation of xylem anatomical traits observed in our study could be related to post-hurricane recovery and overall growth (e.g. canopy filling). Other factors, however, likely decouple a relationship between xylem anatomy and diameter growth. While adjustments of wood anatomy may enable individual trees to capitalize on favorable post-disturbance conditions, these may also influence their future responses or vulnerability to subsequent disturbances.

Zimmerman, J.K.; Aide, T.M.; Rosario, M. [and others]. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management. 77: 65-76. https://doi.org/10.1016/0378-1127(95)03575-U

We compared the long-term effects (60 years) of land use practices and short-term effects (5 years) of a hurricane on forests in abandoned pastures, abandoned coffee plantations, and forested stands in the Luquillo Mountains of eastern Puerto Rico. There was no effect of management practices on species richness of trees and shrubs, nor on species diversity, species evenness, stem density, or basal area. However, there was a strong effect of management on tree species composition. *Myrcia deflexa* and *Palicourea riparia* dominated the former pastures, as well as *Tabebuia heterophylla*, a species which naturally invades pastures and which was subsequently established in many of the pasture areas by the USDA Forest Service. Abandoned coffee plantations were dominated by *Guarea guidonia*. *Cecropia schreberiana*, a pioneer species in the forest, was almost completely lacking in the old pastures indicating that this species is not an important component of forest recovery in abandoned pastures in the Luquillo Mountains. The abundance of *Cecropia schreberiana* in coffee and forest sites was inversely related to distance from the path of Hurricane Hugo (September 1989). Although the recent hurricane strongly affected the forest, it was unable to erase the signature of land use history on the species composition of these sites.

Zimmerman, J.K.; Comita, L.S.; Thompson, J. [and others]. 2010. Patch dynamics and community metastability of a subtropical forest: compound effects of natural disturbance and human land use. Landscape Ecology. 25: 1099-1111. https://doi.org/10.1007/s10980-010-9486-x

Where large disturbances do not cause landscape-wide mortality and successional change, forested ecosystems should exhibit landscape metastability (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.

Zimmerman, J.K.; Covich, A.P. 2007. Damage and Recovery of Riparian Sierra Palms after Hurricane Georges: Influence of Topography and Biotic Characteristics. Biotropica. 39(1): 43-49. https://doi.org/10.1111/j.1744-7429.2006.00237.x

Tropical forests are often shaped by disturbance events, especially in regions where hurricanes and other severe storms occur. We studied the effects of Hurricane Georges (September 1998) on the sierra palm (*Prestoea acuminata var. montana*) in the Luquillo Mountains of Puerto Rico. We established riparian transects along two headwater streams that were similar in size and location, but differed in riparian tree species composition and land-use history. Following Hurricane Georges, sierra palms were surveyed periodically for damage and recovery (measured by initial loss and subsequent regrowth of palm leaves), tree height, sun exposure, and production of inflorescences and infructescences. Palm height had the highest association with damage, with most damage occurring to canopy palms. Palm recovery (4 mo and 10 mo post-hurricane) was associated with high tree density, indicating that sun exposure was not limiting. Hurricane Georges likely reduced production of flowers and fruits in sierra palms for at least 10 mo following the storm, although production of new leaves was rapid. Although palms recovered quickly from defoliation after the hurricane, decreased reproduction resulted in reduced availability of fruit for terrestrial and aquatic consumers.

Zimmerman, J.K.; Everhamm, E.M.; Waide, R.B. [and others]. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. Journal of Ecology. 82(4): 911-922. https://doi.org/10.2307/2261454

The effect of a category 4 hurricane (Hurricane Hugo, 18 September 1989) on subtropical wet forest in Puerto Rico was examined at stand and species levels with respect to the frequency of tree damage, mortality, and resprouting. Data were collected from a 16-ha plot of secondary forest consisting of approximately 13 000 trees > 10 cm DBH representing 88 species. Roughly one-quarter of the trees suffered some type of damage involving the main stem, and mortality due to the hurricane was 9%. Mortality among trees was primarily due to uprooting and broken stems. Many surviving trees sprouted new branches following the hurricane, indicating that this was an important component of stand recovery following hurricane damage. Patterns of species-specific damage and recovery (investigated using 26 common species) appeared to form two distinct groups. One group (`pioneers'), represented by three species, suffered a high frequency of stem breakage and mortality during the hurricane and had a low capacity to sprout new branches after being damaged. The remaining species (`nonpioneers') lost many branches during the hurricane, thereby suffering low to moderate stem damage and mortality, and sprouted many new branches following the hurricane. Stem breakage and related species-specific characteristics were significantly correlated with wood density and shade tolerance. Species exhibited few significant size-specific relationships (using DBH) with respect to hurricane damage, mortality, or resprouting, with the exception of branch damage, which often increased as a function of tree size. The study revealed significant differences among tree species in the degree and type of damage suffered during a hurricane and in the ability to recover from damage and resume a position in the forest canopy. Nonpioneers dominate early in recovery because of the ability to survive a storm and sprout new branches following the storm, while the immediate impact of a hurricane on the abundance of pioneer species is strongly negative.

Zimmerman, J.K.; Hogan, J.A.; Nytch, C.J. [and other]. 2018. Effects of hurricanes and climate oscillations on annual variation in reproduction in wet forest, Puerto Rico. Ecology. 99(6): 1402-1410. https://doi.org/10.1002/ecy.2236

Interannual changes in global climate and weather disturbances may influence reproduction in tropical forests. Phenomena such as the El Nino Southern Oscillation (ENSO) are known to produce interannual variation in reproduction, as do severe storms such as hurricanes. Using stationary trap-based phenology data collected fortnightly from 1993 to 2014 from a hurricane-affected (1989 Hugo, 1998 Georges) subtropical wet forest in northeastern Puerto Rico, we conducted a time series analysis of flowering and seed production. We addressed (1) the degree to which interannual variation in flower and seed production was influenced by global climate drivers and time since hurricane disturbance, and (2) how long-term trends in reproduction varied with plant lifeform. The seasonally de-trended number of species in flower fluctuated over time while the number of species producing seed exhibited a declining

trend, one that was particularly evident during the second half of the study period. Lagged El Nino indices and time series hurricane disturbance jointly influenced the trends in numbers of flowering and fruiting species, suggesting complex global influences on tropical forest reproduction with variable periodicities. Lag times affecting flowering tended to be longer than those affecting fruiting. Long-term patterns of reproduction in individual lifeforms paralleled the community-wide patterns, with most groups of lifeforms exhibiting a long-term decline in seed but not flower production. Exceptions were found for hemiepiphytes, small trees, and lianas whose seed reproduction increased and then declined over time. There was no long-term increase in flower production as reported in other Neotropical sites.

Zimmerman, J.K.; Hogan, J.A.; Shiels, A.B. [and others]. 2014. Seven-year responses of trees to experimental hurricane effects in a tropical rainforest, Puerto Rico. Forest Ecology and Management. 332: 64-74. https://doi.org/10.1016/j.foreco.2014.02.029
Download: https://www.fs.usda.gov/treesearch/pubs/49018

We experimentally manipulated key components of severe hurricane disturbance, canopy openness and detritus deposition, to determine the independent and interactive effects of these components on tree recruitment, forest structure, and diversity in a wet tropical forest in the Luquillo Experimental Forest, Puerto Rico. Canopy openness was increased by trimming branches, and we manipulated debris by adding or subtracting the trimmed materials to the trimming treatments, in a 2 × 2 factorial design replicated in three blocks. Tree (stems >1 cm diameter at breast height) responses were measured during the 9-year study, which included at least 1 year of pre-manipulation monitoring. When the canopy was trimmed, stem densities increased >2-fold and rates of recruitment increased >25-fold. Deposition of canopy debris did not markedly affect stem densities but did have small yet significant effects on tree basal area. Basal area increased about 10% when debris was added to plots with intact canopies; the other treatments exhibited smaller or no increases in basal area over time. Much of the dynamics of stem densities were due to changes in the smallest size class (1–2.5 cm diameter), which responded with a pulse of recruitment in the canopy trimmed treatments, and a steady loss in plots with intact canopies. The decreases in stem densities in the plots with intact canopies is attributed to observed on-going forest thinning from the last natural severe hurricane disturbance in 1998. Given these repeated hurricane effects, our study enabled an experimental test of the Intermediate Disturbance Hypothesis (IDH), for which we predicted an increase in species diversity in canopy trimmed treatments and a loss of species in the treatments with intact canopies. Measured patterns of diversity gave partial support to the predictions of IDH, although raw species richness of sampled plots fit the predictions better than richness adjusted for differences in stem densities among treatments. Ordination of species responses in the community identified a guild of

pioneer species responding to the trimmed treatments, but not the debris additions, amongst substantial background variation in species composition unrelated to the experimental treatments. These results are consistent with a growing consensus that, while trade-offs of resilience and resistance govern many species responses to hurricane disturbance, other environmental and historical factors are equally or more important in governing community dynamics in hurricane-disturbed forests.

Zimmerman, J.K.; Pulliam, W.M.; Lodge, D.J. [and others]. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos. 72(3): 314-322. https://doi.org/10.2307/3546116
Download: https://www.fs.usda.gov/treesearch/pubs/50780

Following damage caused by Hurricane Hugo (September 1989) we monitored inorganic nitrogen availability in soil twice in 1990, leaf area index in 1991 and 1993, and litter production from 1990 through 1992 in subtropical wet forest of eastern Puerto Rico. Experimental removal of litter and woody debris generated by the hurricane (plus any standing stocks present before the hurricane) increased soil nitrogen availability and above-ground productivity by as much as 40% compared to unmanipulated control plots. These increases were similar to those created by quarterly fertilization with inorganic nutrients. Approximately 85% of hurricane-generated debris was woody debris >5 cm diameter. Thus, it appeared that woody debris stimulated nutrient immobilization, resulting in depression of soil nitrogen availability and productivity in control plots. This was further suggested by simulations of an ecosystem model (CENTURY) calibrated for our site that indicated that only the large wood component of hurricane-generated debris was of sufficiently low quality and of great enough mass to cause the observed effects on productivity. The model predicted that nutrient immobilization by decaying wood should suppress net primary productivity for 13 yr and total live biomass for almost 30 yr following the hurricane. Our findings emphasize the substantial influence that woody debris has upon nutrient cycling and productivity in forest ecosystems through its effects on the activity of decomposers. We suggest that the manner in which woody debris regulates ecosystem function in different forests is significantly affected by disturbance regime.