



Arthropods are not declining but are responsive to disturbance in the Luquillo Experimental Forest, Puerto Rico

Timothy D. Schowalter^{a,1}, Manoj Pandey^a, Steven J. Presley^{b,c}, Michael R. Willig^{b,c}, and Jess K. Zimmerman^d

^aDepartment of Entomology, Louisiana State University Agricultural Center, Baton Rouge, LA 70803; ^bInstitute of the Environment, Center for Environmental Sciences & Engineering, University of Connecticut, Storrs, CT 06269-4210; ^cDepartment of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06269-4210; and ^dDepartment of Environmental Sciences, University of Puerto Rico, Rio Piedras, PR 00936-8377

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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 walkingstick 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.

insect decline | hurricane | disturbance | global warming | species turnover

Several long-term studies in Europe and North America have documented declines in important insect groups, notably butterflies, moths, bees, flying beetles, and wood-borers (1–13). These studies have attributed declines to a variety of causes, primarily habitat loss, but also increased insecticide use, light pollution, and climate change, particularly in developed countries in the northern hemisphere. Data adequate for assessing the demographic declines of insects from other regions or from other insect groups in temperate regions are largely lacking (8, 14). The declines of insect abundance and biomass for many higher taxa across multiple sites in northwestern Europe are of a magnitude that threatens the continued delivery of ecosystem services on which humans depend and warrant greater attention and mitigation efforts.

Recently, Lister and Garcia (15) used open access data from the Long-Term Ecological Research Project in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico, supplemented by two of their own collections taken 36 y apart, to claim dramatic declines in total arthropod abundance and biomass (“biomass had fallen 10 to 60 times”) between 1976 and 2012. In addition, they claimed that abundances of insectivorous

frogs, lizards, and birds had declined during this period, leading to food web “collapse.” These declines were attributed to an alleged 2 °C increase in temperature over this time frame. This conclusion was particularly alarming because Lister and Garcia’s (15) report was the first from any tropical region, where as much as 85% of insect diversity may occur (16).

Lister and Garcia’s (15) analytical approach and treatment of the data were questionable, resulting in conclusions that were largely wrong due to the failure to consider disturbance dynamics (17). Although the results of Lister and Garcia (15) have been refuted, a comprehensive and rigorous evaluation of long-term trends for arthropods in the LEF remains to be done, especially as they relate to interacting environmental variation associated with disturbance, succession, and warming. Importantly, hurricane frequency and intensity are highly variable, requiring multiple cycles of disturbance and secondary succession to confidently separate responses to these pulse disturbances from those of long-term and ongoing press disturbances, such as warming.

Our study from the LEF incorporates recent data to extend the long-term record for arthropods to 29 y, during a period that has included multiple major hurricanes and various degrees of forest recovery (succession) after those pulse disturbance events. Previous studies (17, 18) analyzed trends in dynamics following two hurricanes (i.e., Hurricanes Hugo and Georges in 1989 and 1998, respectively). The advent of a third, very intense storm, Hurricane Maria in 2017, facilitated a more robust evaluation of our hypothesis that hurricane-induced disturbance and secondary

Significance

Despite claims to the contrary, arthropod abundances are not generally declining in the Luquillo Experimental Forest in response to warming. Interannual variation in abundance reflects patterns of species turnover as well as consequences of hurricane-induced disturbance and secondary succession. Critically, long-term monitoring using consistent sampling methods over successive years at the same sites is necessary to distinguish long-term trends associated with global warming from punctuated reductions in abundance due to extreme events and successional dynamics.

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¹To whom correspondence may be addressed. Email: tschowalter@agcenter.lsu.edu.

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succession drive changes in arthropod abundance in the LEF, rather than climate warming (15). We are interested in both the direct effects of climate change as represented by rising temperatures as well as indirect effects of climate change as manifested by increased frequency or intensity of disturbance through hurricanes (19, 20). Using these new data, our objectives are to characterize long-term trends in arthropod abundance and to determine the degree to which interannual variation in abundances is associated with effects of repeated hurricane-induced disturbances or temperature variation in tropical montane forest in Puerto Rico.

Results

Ambient temperature did not change consistently through time ($P = 0.112$, $r^2 = 0.013$, $B_1 = 0.006$), whereas understory temperature exhibited a significant (significance throughout this paper was judged at $\alpha = 0.05$) negative relationship ($P = 0.017$, $r^2 = 0.208$, $B_1 = -0.047$) with year (SI Appendix, Fig. S1). This negative temporal trend of understory temperature (i.e., cooling) is associated with forest recovery after Hurricane Hugo (17), but with a notable increase in temperature after the removal of forest canopy by Hurricane Maria. Indeed, post-Maria temperatures are similar to those after Hurricane Hugo (SI Appendix, Fig. S1). The effect of secondary succession contributed to a lack of correlation between ambient and understory temperatures ($r = 0.161$, $P = 0.211$).

Walkingsticks exhibited a significant negative temporal trend ($P = 0.001$, $r^2 = 0.457$, $B_1 = -0.058$) in abundance in the LEF (Fig. 1). Total abundance of canopy arthropods exhibited significant temporal trends on each of the six host tree species (Fig. 2), with positive trends on *Casearia arborea*, *Cecropia schreberiana*, and *Dacryodes excelsa*, and negative trends on *Manilkara bidentata*, *Prestoea acuminata*, and *Sloanea berteriana* (SI Appendix, Table S1). For analyses restricted to abundant taxa of canopy arthropods, taxa increased in abundance through time in 17

cases, decreased in abundance through time in 9 cases, and exhibited no consistent response through time in 17 cases (SI Appendix, Table S1). In general, different taxa on the same host tree species exhibited different temporal responses and the same taxa on different host tree species exhibited different temporal responses (SI Appendix, Tables S1 and S3).

Walkingstick abundance responded significantly to both hurricane identity ($P < 0.001$) and time after most recent major hurricane (TAH; $P = 0.001$), but not to their interaction ($P = 0.583$) or to either aspect of temperature (ambient temperature, $P = 0.319$; understory temperature, $P = 0.139$), based on a generalized linear model (GLM). Subsequent analyses designed to isolate the effects of significant components showed that walkingstick abundances were significantly greater after Hurricane Hugo (mean abundance per survey = 26.6) than after Hurricanes Georges (mean abundance per survey = 9.1) or Maria (mean abundance per survey = 11.0). In addition, walkingstick abundances consistently decreased with TAH ($B_1 = -0.075$, $P = 0.024$) after accounting for effects of hurricane identity, ambient temperature, and understory temperature. Despite using Gaussian rather than a negative binomial error term and exploring shared variation partitions rather than an interaction between hurricane identity and TAH, variation partitioning (Fig. 3 and SI Appendix, Table S2) largely confirmed results of the GLM, with significant unique partitions for hurricane (adjusted $r^2 = 0.387$, $P = 0.006$) and for understory temperature (adjusted $r^2 = 0.109$, $P = 0.038$), with a significant overall model (adjusted $r^2 = 0.412$, $P = 0.007$).

Total canopy arthropod abundance exhibited at least one significant response to hurricane effects on four of six host species (hurricane identity on *C. schreberiana* and *D. excelsa*; TAH on *D. excelsa*; hurricane by TAH interaction on *M. bidentata* and *P. acuminata*), with no significant effects of temperature (SI Appendix, Table S3). Similarly, hurricane effects explained more variation than did ambient or understory temperature in

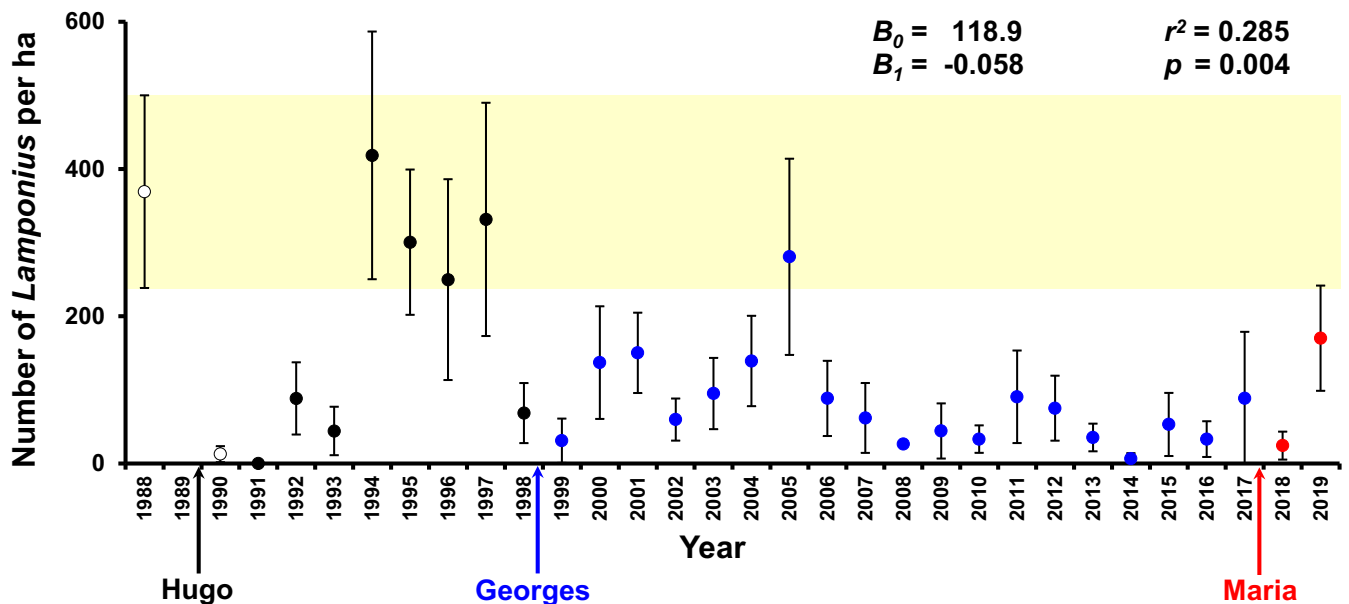


Fig. 1. Abundances of the walkingstick, *Lamponius portoricensis*, during 1988 to 2019 in tabonuco forest at the LEF, Puerto Rico. Data for 1991 to 2019 (solid circles) are from the Luquillo Forest Dynamics Plot (LFDP) during the wet season. Because no comparable earlier data exist for the LFDP, data for 1988 and 1990 (open circles), immediately before and after Hurricane Hugo, are from a grid in the nearby Bisley Watersheds during the wet season. The most recent high-intensity hurricane before Hurricane Hugo to impact the LEF was Hurricane Betsy in 1956. Consequently, we used data immediately before Hurricane Hugo to represent a putative base line (yellow band represents mean abundance +2 SE) for assessing long-term patterns. Black, blue, and red circles represent data following Hurricanes Hugo (1989), Georges (1998), and Maria (2017), respectively. Results of linear regression (intercept, B_0 ; slope, B_1 ; coefficient of determination, r^2 ; significance, P) show the response of walkingstick abundance to time in the LFDP.

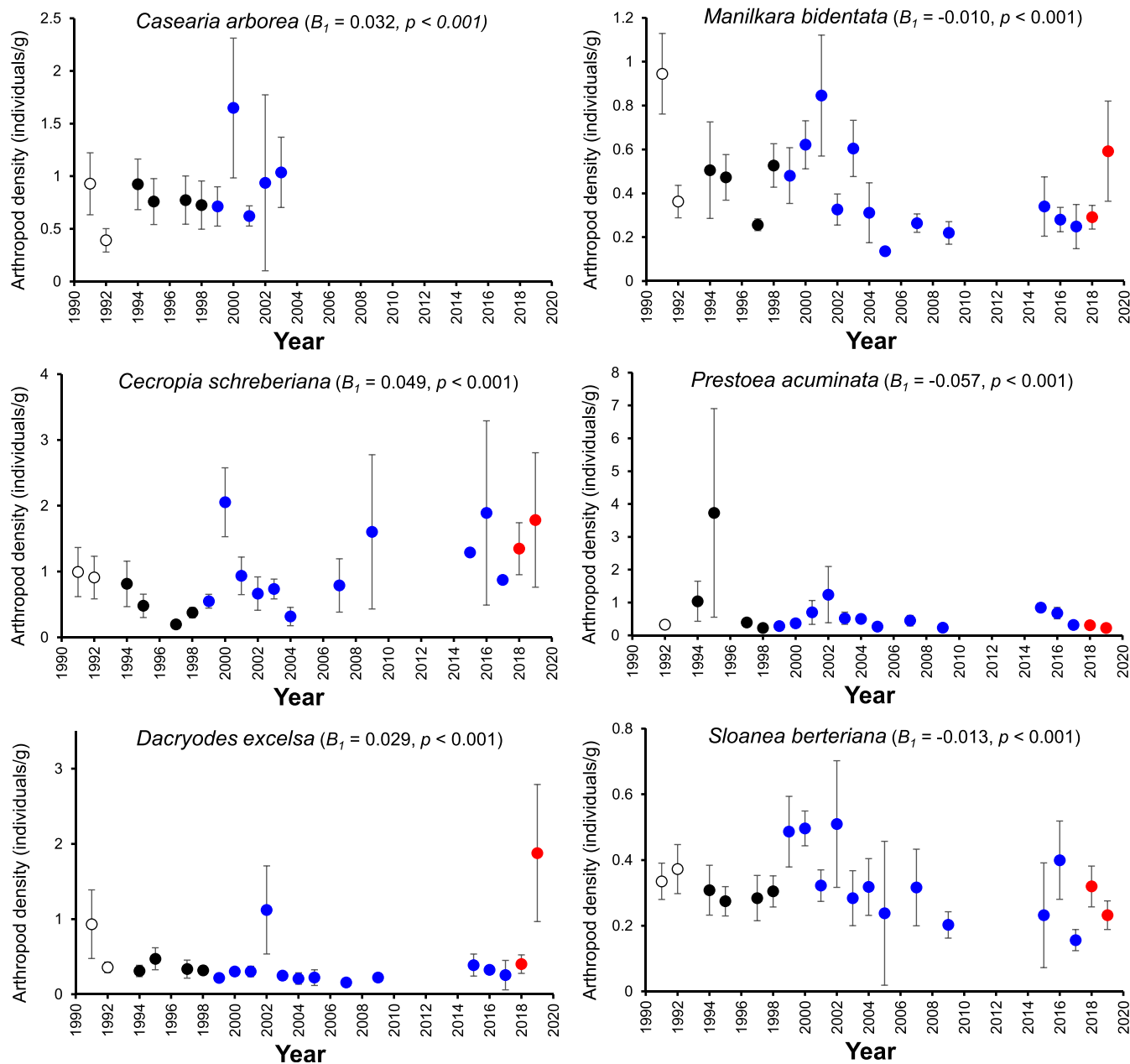


Fig. 2. Mean total arthropod density (individuals per gram of foliar mass) from each of six tree species for each year from 1991 to 2019 at the LEF in Puerto Rico. Densities after Hurricanes Hugo (1989), Georges (1998), and Maria (2017) are represented by black, blue, and red circles, respectively. Open circles are data after Hurricane Hugo that were not included in generalized linear mixed-effects models because reliable understory temperature data were not available for those years. Error bars represent ± 1 SE. Regression coefficients (B_1) and associated statistical significance (P) are from GLMMs, each with a negative binomial error term that evaluated responses of total arthropod abundance to year, using sample foliar mass as an offset, and experimental block and historical legacy as random effects to control for spatiotemporal variation. Arthropod densities increased on three tree species (*C. arborea*, *C. schreberiana*, and *D. excelsa*) and decreased on three tree species (*M. bidentata*, *P. acuminata*, and *S. berteriana*) during this time period.

each variation partition analysis (i.e., *C. schreberiana*, *D. excelsa*, and *M. bidentata*) of total abundance for which significant effects characterized variability (SI Appendix, Table S4).

Abundance exhibited at least one significant response to hurricane identity, ambient temperature, understory temperature, TAH, or hurricane by TAH interaction in 23 of 43 combinations of arthropod taxon and host tree species (SI Appendix, Table S3). In 19 cases, taxon abundance exhibited at least one response to a hurricane effect, in 14 cases taxon abundance exhibited at least one response to temperature, and in 10 cases taxon abundance exhibited at least one response to both hurricane

and temperature (SI Appendix, Table S3). Subsequent analyses designed to isolate particular factors indicated that abundances were greater more often after Hurricane Maria (eight cases) than after Hurricane Hugo (six cases) or after Hurricane Georges (one case). Abundances declined with time after the most recent major hurricane more often (nine cases) than they increased (five cases) with time after the most recent major hurricane. Abundances were equally likely to respond positively (nine cases) or negatively (nine cases) to increases in temperature. Results generally were consistent with those based on generalized linear mixed-effects models (GLMM). More specifically, unique

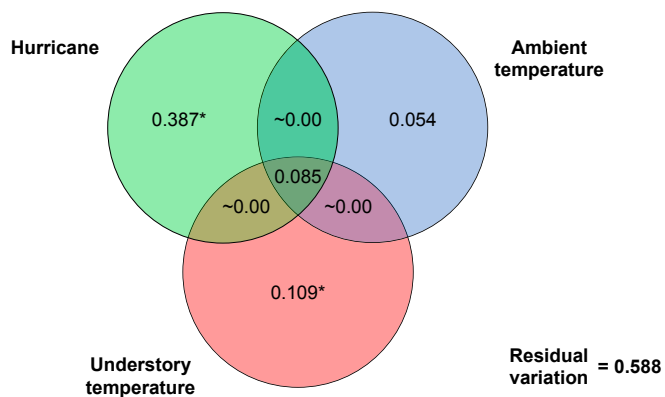


Fig. 3. Variation partitioning for mean abundance of *L. portoricensis* from the LFDP during 1993 to 2019. The full model significantly accounted for 41.2% of the interannual variation in abundance. Partitions included hurricane, represented by hurricane identity (Hurricanes Hugo, Georges, Maria) and time after hurricane, ambient temperature (mean daily maximum temperature for each year), and understory temperature (mean daily maximum temperature for each year). The unique effect of a partition appears in the corresponding nonoverlapping portion of each circle, and the total effect of a partition is displayed outside each corresponding circle. Numerical values are explained amounts of variation related to partitions or models; significant effects are indicated by an asterisk.

hurricane effects were twice as common as unique ambient or understory temperature effects. Moreover, total hurricane effects were three times more common than were total ambient or total understory temperature effects (*SI Appendix, Table S4*).

Discussion

Walkingstick Trends. Long-term dynamics of walkingstick abundance (Fig. 1) are determined primarily by hurricane-induced disturbance and the trajectory of forest succession after each hurricane. Each of the three major hurricanes to impact the LEF since 1989 were unique in the extent and severity of the damage caused to the forest, as well as with respect to the successional sere characterizing the forest at the time of hurricane impact (21–23). Nonetheless, a reduction in walkingstick abundance is evident immediately following each hurricane (Fig. 1). After each hurricane, this decline is followed by a rapid increase in abundance, followed by decreases (note that, to date, only the immediate decrease and ensuing rapid increase have occurred with respect to Hurricane Maria). In general, abundance of *Lamponius portoricensis* is highly associated with the availability of plants on which they forage, and these plants are predominantly early successional shrubs and understory saplings (e.g., *Piper hispidum*, *Piper glabrescens*, *Urera baccifera*, and *Dendropanax arboreus*) (24, 25). *L. portoricensis* reaches its greatest densities in successional forest or small light gaps in otherwise closed-canopy forest (25, 26). Consequently, its densities over the past few decades were greatest from 1994 to 1997, during succession following Hurricane Hugo. Early responses after Hurricane Maria suggest that walkingstick abundances again are increasing during early stages of forest succession (Fig. 1).

Understory temperatures at the LEF are affected by canopy loss (27, 28), with the highest understory temperatures over the past 30 y recorded soon after Hurricanes Hugo and Maria (*SI Appendix, Fig. S1*), the hurricanes that removed large portions of the forest canopy. Variation partitioning showed that understory temperature explains a significant portion of unique variation beyond that accounted for by hurricane effects (Fig. 3 and *SI Appendix, Table S2*). This further suggests that responses of walkingsticks to disturbance and successional trajectories are complex, and likely arise from interactions between temperature

change, interval of recurring high-intensity hurricanes, and their effects on density and distribution of plants on which walkingsticks forage (29).

The flora and fauna in the LEF likely are adapted to survive variation in temperature of a magnitude greater than that currently realized by climate change. The LEF is largely a hurricane-mediated ecosystem, and hurricane-induced loss of forest canopy increases the temperature experienced by understory arthropods more than has global warming, at least to date [see supplementary figure S2 in Willig et al. (17)]. For example, the mean daily maximum temperature increased by 3.26 °C from the 365 d before Hurricane Maria compared to the 365 d after the hurricane, whereas estimates of warming for Puerto Rico suggest an increase of only 0.02 to 0.024 °C per year (17), which would require 130 to 160 y to match the change in understory temperature caused by nearly complete loss of the forest canopy due to Hurricane Maria. This does not mean that temperature change has no effect on these systems, only that the resistance and resilience of LEF arthropods to temperature fluctuations will make detection of such responses difficult and may only appear after greater increases in temperature than those currently experienced by Puerto Rico. Importantly, climate change may affect arthropods in the LEF via an increase in hurricane frequency (30), which may truncate long-term successional trajectories of populations and communities. For example, Hurricane Georges impacted the LEF only 9 y after Hurricane Hugo, affecting secondary post-Hugo succession of the forest and the trajectories of arthropod populations (e.g., Fig. 1).

Similar changes in abundance over this time period have been observed for gastropods, insectivorous frogs, and birds at the LEF, demonstrating consistent faunal responses to disturbances at this site regardless of taxon (17, 30, 31). Insectivorous frogs and birds have not declined over time as claimed by Lister and Garcia (15), but rather showed similar pulses in abundance after hurricanes, followed by several years of slow decline toward baseline levels [see supplementary figures S9–S11 in Willig et al. (17) for data on frogs and birds]. Interpretation of long-term trends is sensitive to timing of initiation and duration of sampling in disturbance-mediated systems (32). In addition, multiple cycles of disturbance and succession are required to confidently separate responses to pulse disturbances (hurricanes) vs. press disturbances (warming).

Canopy Arthropod Trends. In contrast to many studies (1–10) that have led to claims of an “Insectageddon,” long-term data for canopy arthropods do not show consistent declines in abundance through time (Fig. 2). Rather, abundances on particular host trees are as likely to have increased over the past three decades as they are to have decreased (*SI Appendix, Table S1*). Regardless of the potential mechanisms (climate change versus disturbance and secondary succession) one may wish to invoke as an explanation of long-term trends of these arthropods, no evidence suggests that canopy arthropods in the LEF are consistently declining in abundance through time. Unlike many locations in which declining insect abundances have been recorded (1–10), the LEF is not subject to land-use change, large-scale pesticide use, or habitat loss. What does occur in the LEF is repeated large-scale and severe disturbances associated with hurricanes that result in secondary succession that takes decades to produce a closed canopy forest. Our consideration of long-term data that incorporated multiple cycles of disturbance are the kind of rigorous data and analyses necessary to evaluate claims of mass insect loss (33) in such disturbance-mediated systems. Moreover, the large sample sizes and time period represented by these data are necessary to distinguish among multiple potential mechanisms that may be confounded in space or time.

If direct effects of global warming were a dominant and pervasive factor effecting declines in arthropod abundance in the

LEF (as opposed to the indirect effects associated with particular hurricanes or subsequent secondary succession), we would expect to see a number of consistent demographic patterns: 1) Total abundances of arthropods would be declining on each host tree species; 2) abundances of many arthropod taxa on the same host tree would be declining and would do so on each host tree species; and 3) abundances of many arthropod taxa would be declining on every host tree on which they occur, rather than showing host tree-specific responses. Similarly, we would expect ambient temperature to significantly affect interannual variation in the abundances of many, if not most, combinations of arthropod taxon and host tree species. Empirical results failed to corroborate any of these predictions. First, temporal trends in total abundance of arthropods increased over time as often as they decreased over time, depending on host tree species (Fig. 2). Second, temporal variation in abundance of particular arthropod taxa was highly variable within each host tree species (*SI Appendix, Table S1*), some taxa increasing, some taxa decreasing, and some taxa varying at random with respect to time (e.g., on *C. schreberiana*: Colembola spp. and mealybugs significantly increased over time; coccinellid beetles decreased over time; and *Cyrtoxipha gundlachi* and *Wasmannia auropunctata* did not significantly vary over time). Third, temporal responses of particular arthropod taxa depended on host tree species (*SI Appendix, Table S1*), increasing on some host tree species, decreasing on some host tree species, and varying at random with respect to time on some host tree species (e.g., *W. auropunctata* increased over time on *C. arborea*, decreased over time on *P. acuminata*, and did not significantly vary over time on *C. schreberiana*, *D. excelsa*, *M. bidentata*, and *S. berteriana*). Finally, variation in ambient temperature did not significantly affect total arthropod abundance on any host tree species, whereas factors related to hurricane disturbance and secondary succession (i.e., hurricane identity, TAH, understory temperature, and the interaction between hurricane identity and TAH) affected variation in total arthropod abundance on four of six host trees (*SI Appendix, Tables S3 and S4*). Ambient temperature played a minor and secondary role influencing only taxon-level arthropod abundances, and was just as likely to result in an increase in taxon abundance as it was to result in a decrease in taxon abundance.

Schowalter et al. (18) demonstrated that the canopy arthropod community at LEF sampled at any point in time reflects the legacy of species turnover and community recovery following previous disturbances, each of which filtered the surviving community in different ways. The 29 y of canopy arthropod data confirm that total abundances on particular host tree species peak following hurricanes, followed by several years of steady decline, with the exception of arthropods on *P. acuminata* (Fig. 2).

The most recent data for canopy arthropods indicate that abundance in 2019 equaled or exceeded that in 1991, the previous maximum in the record for the LEF (excluding an exceptionally high abundance in 2002 that reflected a high density of mealybugs on *C. schreberiana*). Importantly, peaks in arthropod abundance generally occurred during the early stages of succession after a major hurricane-induced disturbance event. This suggests that abundances of insect faunas in montane forests in Puerto Rico are dynamic and are influenced by dramatic changes to local environmental conditions associated with hurricanes and posthurricane secondary succession (Fig. 2). These changes include rapid resprouting and refoilation of recovering trees, which provide abundant resources for sap-suckers, and abundant detrital material, which provides resources for detritivores, thereby fueling increased abundances of these functional groups (34). Similar postdisturbance responses have been observed in other forest types (35–37). In addition, the increases in abundance of these functional groups provide resources for spiders and other arthropod predators. Chewing herbivores are sensitive to changes in host conditions, especially defensive chemistry, resulting from

disturbance (37), with responses to changes in plant condition differing widely among herbivore taxa (38).

Not surprisingly, hurricane-induced disturbances resulted in substantial species turnover, reflecting declines in some taxa and their replacement by other taxa following Hurricane Georges, and perhaps in the future during succession after Hurricane Maria. The 10 most abundant taxa for 1991 to 2001 included 4 scale insects (*Ceroplastes rubens*, *Coccus acutissimus*, *Protospulvinaria pyriformis*, and *Vinsonia stellifera*), tree crickets (*C. gundlachi*), collembolans, coccinellids, little fire ants (*W. auropunctata*), cockroaches (primarily *Cariblattoides guava*), and salticid spiders (primarily *Lyssomanes portoricensis*). The 10 most abundant taxa for 2009 to 2019 included 7 taxa that were among the 10 most abundant for both time periods. However, *V. stellifera*, coccinellids, and salticid spiders were replaced among the 10 most abundant taxa for 2009 to 2019 by mealybugs, microlepidopterans, and psocoptera.

Cautions and Recommendations for Long-Term Research. Our results do not suggest that arthropod declines are not occurring in other regions, including those in the tropics (12, 14, 39–41), only that previous reports of declines in Puerto Rico associated with global warming should not be accepted without careful consideration of the complexities of disturbance and succession that arise from hurricane-induced disturbance and subsequent secondary succession (14, 18, 33, 42, 43). Declines of some insects and other groups have been documented and are especially concerning because of the linkage of these organisms to critical ecosystem functions and services (5, 7, 11, 44, 45). However, the extent of declines is still unknown (43). Moreover, false claims can initiate undue alarm or may suggest erroneous underlying causes that together undermine the credibility of science (32, 43). Clearly, more long-term studies, as well as studies of longer duration than currently exist, are needed to evaluate the underlying mechanisms responsible for trends in arthropod abundance, with particular attention devoted to the ultimate consequences for food webs and ecosystem services (11, 32).

Consistent sampling over time is necessary to track trends (e.g., refs. 4, 5, 7, and 33). When two sampling periods are separated by multiple decades (15, 46), it is challenging, if not impossible, to distinguish a long-term trend from punctuated reductions due to extreme events (42). Studies that represent multiple snapshots in time often provide incomplete or misleading impressions of long-term dynamics, associations with mechanisms, or the effects of disturbance on the biota (11, 32, 44, 47). The conclusions of Lister and Garcia (15) also highlight the importance of nonarbitrary start and end dates when using long-term monitoring studies to address questions that the data were not intended to answer. Data in the LEF were collected to evaluate long-term responses to hurricane-induced disturbances. As such, the time series represents the successional stages of forest recovery after major hurricanes. The LEF data used in Lister and Garcia (15) characterized forest succession from 2 y after Hurricane Hugo until a closed canopy had regrown, rather than characterizing a closed canopy forest only exposed to temperature changes. Consequently, they ignored hurricane-mediated disturbance and succession, and confounded their evaluation of the direct effects of temperature change.

Organisms are arguably more sensitive to extreme events than to mean conditions (48). Insects and other heterothermic organisms are particularly sensitive to extreme temperatures or moisture levels. For example, a low winter temperature exceeding tolerance ranges can reduce arthropod abundances prior to sampling the next year, regardless of long-term trends in temperature or abundance (42). Furthermore, abundances of many species peak at intervals of one to several decades in response to disturbances (35) or because of time lags in predator–prey cycles (49). Consequently, evaluations of trends in insect abundance

are sensitive to sampling frequency and duration. Sampling periods could show a variety of demographic trends depending on start and end dates relative to disturbance intervals or population cycles (32). Therefore, consistent sampling for 30 y or more may be necessary to provide credible data on causes of long-term trends, especially for populations occupying disturbance-mediated environments such as the LEF. The same or similar sites must be sampled consistently over time to avoid geographic artifacts. Arthropod abundances can differ substantially from one plot to another due to differences in habitat, food quality, or disturbance legacies (50). Even plots separated by only 10 to 20 m can differ in disturbance legacies and arthropod abundances (34). Importantly, disturbance intensities or habitat characteristics can differ among sites at small spatial scales because of topographic and edaphic features of the landscape, creating considerable environmental heterogeneity. Consequently, many replicates are required to distinguish long-term demographic trends from successional turnover associated with episodic events. This is even more critical as hurricane frequency could increase by a factor of 5 in the Caribbean if significant reductions in carbon emission are not curtailed even more than recommended in the Paris Agreement (19, 20).

Conclusions. Despite the lack of strong evidence for pervasive declines in arthropods in Puerto Rico, or the linkage of variability in abundance to variation in ambient temperature, we reiterate that we are in the midst of a biodiversity crisis. Sufficient information exists about the effects of habitat loss, fragmentation, climate change, and land-use intensity to take action to protect and restore habitats for organisms that are responsible for critical ecosystem processes, such as pollination, decomposition, and biological control (43). Many species are being lost due to habitat destruction, especially in the tropics, where as much as 85% of insect diversity may be represented (16). In most cases, population declines are indicative of changes that could threaten the production and delivery of ecosystem services on which humans depend for survival. Such warnings should be followed by careful and expanded assessments of trends to ensure that the underlying mechanistic bases for the declines are understood.

Methods

Site Description. Research was conducted in the Luquillo Experimental Forest (18°10'N, 65°30'W) in the Luquillo Mountains of Puerto Rico (51). Tabonuco forest is the dominant forest type below 600 m in the LEF. Mean monthly temperatures range from 25 °C in January to 27 °C in September (52). Precipitation averages 3,668 mm per year and varies seasonally, with 200 to 250 mm per month in January to April and 350 to 400 mm per month in the remainder of the year (53, 54).

The LEF is subject to frequent hurricanes that alter the composition of forest communities (55). Prior to 1989, Puerto Rico had not experienced a major hurricane (greater than or equal to category 3 storms) for 33 y (Betsy in 1956) and a closed canopy characterized the forest. However, during the last few decades, three major hurricanes (Hugo in 1989, Georges in 1998, and Maria in 2017) have passed over eastern Puerto Rico. Each produced considerable damage to the LEF, but the three hurricanes differed in intensity, extent, and severity. Hurricane Hugo, a strong category 3 storm with maximum sustained winds of 227 km/h, produced large canopy openings and deposited much debris on the forest floor (21). Hurricane Georges, a category 3 storm with sustained winds of 177 km/h (22), caused extensive defoliation of trees but did not produce large quantities of coarse woody debris. Hurricane Maria, a strong category 4 storm with sustained winds of 250 km/h, caused extensive tree mortality and canopy opening over much of the LEF, and deposited large amounts of woody debris on the forest floor (23).

Temperature Data. To estimate effects of global warming, we used data provided by the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration from the station at the Luiz Muñoz Marín International Airport in San Juan, Puerto Rico (Network ID: GHCND:RQW00011641). To estimate annual ambient temperature in the

northeastern region of Puerto Rico, we averaged the daily maximum temperatures for each year (hereafter “ambient temperature”).

One of the effects of hurricane-induced disturbances on tropical forests is a change in the understory climate precipitated by removal of the forest canopy (25, 26). Subcanopy temperatures in the LEF can be influenced by both global warming and by the state of the forest canopy due to loss of canopy cover and ensuing succession. Subcanopy temperatures are those experienced by canopy arthropods and walkingsticks, whose responses we evaluate here. There was an instrument failure at the weather station in the LEF that resulted in an underestimate of maximum daily temperatures from 1988 to 1992. The instrument was replaced, providing a reliable estimate of maximum daily temperatures from mid-1992 until the present. Consequently, all analyses considered only data from 1993 to 2019 to standardize the time frame of analysis and to ensure accurate estimates of the understory temperature. To estimate annual temperature below the forest canopy, we averaged daily maximum temperatures from the weather station located in the forest understory in the LEF for each year (hereafter “understory temperature”).

Arthropod Sampling. Walkingsticks (*Lamponius portoricensis*) were surveyed annually from 40 points on the Long-term Forest Dynamics Plot (LFDP) in the LEF from 1991 through 2019. At each point, all surfaces in a circle of 3-m radius (up to 3 m of height) were inspected for walkingsticks. The same 40 points were surveyed four times during most years, but only twice in 1993 and three times in 1994 due to logistical constraints. To account for this variation in number of surveys, we used the mean number of walkingsticks per survey each year as the response variable for analyses of long-term trends in walkingstick abundance (i.e., the mean is not biased with respect to number of samples). For sampling details, see Willig et al. (27, 56).

To sample canopy arthropods, six blocks were established in 1991 over an 11-ha area at about 380 m of elevation (57). Each block included paired plots representing a canopy opening created by Hurricane Hugo and closed canopy forest (i.e., disturbance legacy). Samples were collected from foliage during 1991 to 1992, 1994 to 1995, 1997 to 2005, 2007, 2009, and 2015 to 2019. Only samples collected during the wet season (May to July) were used to avoid potential effects of seasonal variation in arthropod incidence or abundance. Six host tree species were selected for study to represent dominant early (*C. arborea*, *C. schreberiana*) and late (*D. excelsa*, *M. bidentata*, and *S. berteriana*) successional species, as well as overstory (*D. excelsa*, *M. bidentata*, *S. berteriana*, and *C. schreberiana*) and understory (*C. arborea* and *P. acuminata*) trees. Consequently, any variation in arthropod abundance is not a characteristic of the forest as a whole and must be interpreted only with regard to the particular host tree species (i.e., combining data for these host tree species is untenable). One tree of each species was sampled in each plot at each sample time. In each plot at each sampling time, one accessible branch was collected from one randomly chosen tree of each host species (if present). Branches were usually ~50 cm in length and no more than 1 cm in diameter at the point of excision.

Foliage from samples was pressed and dried at 50 °C to constant weight to provide a measure of sample mass for use as an offset in statistical analyses. All arthropods in each sample were identified to the lowest possible taxonomic rank. Abundant or well-known taxa were identified to genus or species by specialists at the US Department of Agriculture Systematic Entomology Laboratory in Beltsville, MD. Most taxa were identified to genus or family by the senior author. For additional details on experimental design and sampling, see Schowalter and Ganio (57, 58) and Schowalter et al. (18).

Quantitative Analysis. Simple linear regression was used to evaluate consistent temporal trends in ambient or understory temperature. For each analysis, mean maximum daily temperature was the dependent variable and year was the independent variable.

For each group (walkingsticks or canopy arthropods), we first evaluated temporal trends in abundance. Second, we evaluated factors related to hurricane-induced disturbance and global warming that may account for interannual variation. Finally, we used variation partitioning to quantify the unique and shared variation associated with hurricane-related factors and two aspects of temperature.

To evaluate long-term trends in walkingstick abundance, we conducted a GLM with a negative binomial error term, mean number of walkingsticks per survey as the response variable, and year as the explanatory variable. A pseudo r^2 for this GLM was calculated using the rsquared function from the piecewiseSEM library in R (59).

To evaluate long-term trends in canopy arthropod abundance, we conducted separate GLMMs for each combination of host tree species and

arthropod taxon, as well as for each combination of host tree species and total arthropod abundance. Only taxa that occurred in at least 10% of samples from a particular host tree species were used in the former analyses. Each analysis used arthropod abundance as the response variable with sample foliar mass as an offset, a negative binomial error term, experimental block and historical legacy (i.e., gap or nongap habitat after Hurricane Hugo) as random effects, and year as the explanatory variable.

To determine if disturbances associated with hurricanes or temperature influence long-term trends in walkingstick abundance, we conducted a GLM with a negative binomial error term, mean number of walkingsticks per survey as the response variable, hurricane identity (i.e., each year was coded as having occurred after a particular hurricane but before a subsequent hurricane, such that "Hugo" was the time between Hurricanes Hugo and Georges, "Georges" was the time between Hurricanes Georges and Maria, and "Maria" was the times after Hurricane Maria), TAH in years, ambient temperature, understory temperature, and a hurricane by TAH interaction as explanatory variables using type II sums of squares. A pseudo r^2 for this GLM was calculated using the r -squared function from the piecewiseSEM library in R.

To determine if disturbances associated with hurricanes or climate change influence long-term trends in canopy arthropod abundance, we conducted GLMMs with a negative binomial error term, abundance as the response variable, foliar mass of sample as an offset, experimental block and historical legacy as random effects, and hurricane identity (Hurricane Hugo, Georges, or Maria), TAH, ambient temperature, understory temperature, and a hurricane by TAH interaction as explanatory variables using type II sums of squares. Analyses were conducted separately for each combination of host tree species and arthropod taxon, as well as for host tree species and total arthropod abundance. In addition, only taxa that occurred in at least 10% of samples from a particular host tree species were analyzed for taxon-specific responses of particular arthropod taxa on particular host tree species.

Pseudo post hoc analyses were conducted to isolate the effect associated with each explanatory variable evincing a significant effect on walkingstick abundance. A GLM with a negative binomial error term using ambient temperature, understory temperature, and TAH as offsets isolated effects of hurricane identity on mean walkingstick abundance. A Tukey test with a Holm-Šidák adjustment was used to identify differences between all possible pairs of hurricanes. A GLM with a negative binomial error term using ambient and understory temperatures as offsets and hurricane identity as a covariate isolated effect of TAH on mean walkingstick abundance. A pseudo r^2 for this GLM was calculated using the r -squared function from the piecewiseSEM library in R.

Pseudo post hoc analyses were conducted to isolate the effect associated with each explanatory variable evincing a significant effect on taxon-specific or total canopy arthropod abundance. For each significant effect of hurricane identity, a GLMM with a negative binomial error term using foliar mass, ambient temperature, understory temperature, and TAH as offsets and experimental block and historical legacy as random effects isolated effects of hurricane identity on mean canopy arthropod abundance. A Tukey test with a Holm-Šidák adjustment was used to identify differences between all possible pairs of hurricanes from each GLMM. For each significant response to ambient temperature, understory temperature, or TAH, a GLMM with a negative binomial error term using foliar mass as well as the remaining continuous variables as offsets (e.g., for an analysis isolating the effects of ambient temperature both understory temperature and TAH were used as offsets), experimental block and historical legacy as random effects, and hurricane identity as a covariate isolated effects of ambient temperature, understory temperature, or TAH on mean canopy arthropod abundance. These analyses were conducted primarily to determine the direction of response (i.e., abundance increasing or decreasing with increasing temperature or TAH) of canopy arthropod abundance.

Variation partitioning was used to determine the unique and shared variation in walkingstick or canopy arthropod abundance explained by hurricane effects (hurricane identity and TAH), ambient temperature, and understory temperature. Because variation partitioning does not allow for inclusion of offsets, residuals were extracted from a linear regression of abundance and foliar mass separately for each combination of host tree species and total arthropod abundance, as well as for each combination of host tree species and taxon-specific abundance. Although we could use residuals to account for effects of foliar sample mass, variation partitioning cannot deal with such complex models and does not allow for use of negative binomial distributions or random effects that were included in the associated GLMMs. This likely reduces the ability of the analysis to explain variation in arthropod abundance, but we considered the ability to partition total and unique effects a valuable companion to the GLMs and GLMMs. Analyses were conducted only for GLMMs that exhibited at least one significant effect on walkingstick or canopy arthropod abundance. Redundancy analyses determined the significance of each unique partition, each total partition, and the overall model. Significance of shared partitions cannot be determined statistically (60, 61).

All GLMs were conducted using the `glm.nb` function from the MASS package (62); all GLMMs were conducted using the `glmer.nb` function from the lme4 package (63), and variation partitioning was conducted using the `varpart` function from the vegan package (64) in R. Type II sums of squares were implemented via the ANOVA function in the car package (65). All analyses were conducted in R v3.6.1 (66).

The scale of interest in these long-term trends is that of the forest, rather than at the plot or individual host tree scale. Moreover, no spatial variation in explanatory variables (e.g., year, hurricane identity, time after most recent major hurricane, ambient temperature, understory temperature) was available, which prevents any effective evaluation of microspatial variation in this context. Because each survey of walkingsticks represented the same effort and experimental design (i.e., the same 40 points), analyses of walkingstick data could be conducted with all data combined for each year. In contrast, because canopy arthropod samples did not represent the same effort (i.e., variation in foliar mass of sample) or combination of experimental blocks and historical legacy (i.e., all tree species did not occur in all experimental blocks every year due to succession and temporal dynamics), analyses at the sample level were required to properly account for annual variation in each of these factors and the structure of the data (i.e., count data requiring a negative binomial error term with foliar mass as an offset). Use of density in these analyses is less desirable because all abundances of zero are not equivalent (i.e., no individuals from a 5-g sample of foliar mass is not equivalent to no individuals from a 50-g sample of foliar mass).

All data are from the NSF-supported Luquillo Long-Term Ecological Research Site. Data are archived publicly in accordance with NSF guidelines. These data are from Datasets 96 (<https://luq.lter.network/data/luqmeta-data96>) and 107 (<https://luq.lter.network/data/luqmetadata107>).

Data Availability. All study data are included in the article and supporting information.

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