

# Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest

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In PNAS, Lister and Garcia (1) report declines in abundances of understory arthropods and lizards between 1976 and 2012 and claim similar declines in populations of arthropods, frogs, and insectivorous birds based on data from the Luquillo Long-Term Ecological Research project (LUQ). Their conclusion, that increasing temperature has led to a collapse of the food web, has attracted considerable attention from public media, but this conclusion is not corroborated by empirical evidence from LUQ (see Supplementary Materials, <https://luq.lter.network/pop-trends-yunque-luquillo>). Also, the authors fail to consider the effects of hurricanes and subsequent changes during secondary succession.

Lister and Garcia (1) interpret temporal changes in abundance of the walking stick (*Lamponius portoricensis*), canopy arthropods, frogs (*Eleutherodactylus coqui*), and birds at El Verde to be a consequence of increasing annual mean maximum daily temperature. In many cases, abundance data are not adjusted to consider variation in sampling effort. Moreover, the authors combine data files that are not compatible to create the temperature record for analyses. Indeed, maximum temperature from this record evinces a significant linear decrease at El Verde (cooling) in the period during which Lister and Garcia analyzed demographic data, a pattern evident in figure 1A of ref. 1 (see figures 1 and 2 of Supplementary Materials).

Using Lister and Garcia's (1) analytical approach for temporal trends, we found a significant decline in density of *Lamponius* from 1993 to 2011, but density was not statistically related to temperature during this period (figures 3 and 4 of Supplementary Materials). These results contradict those of Lister and Garcia and suggest a more complex interplay of factors affecting variation in abundance of *Lamponius* (2). Canopy arthropod density does not decline between 1994 and 2009 but does increase significantly with increasing temperature (figures 5 and 6 of Supplementary Materials), even for the 10 most abundant taxa (tables

1 and 2 of Supplementary Materials), which Lister and Garcia claimed to have used (3).

Long-term data do not suggest a simple decline in adult frogs from 1987 to 2017 (figure 7 of Supplementary Materials) but do document an increase in numbers with increasing temperature (figure 8 of Supplementary Materials). Numbers vary in a consistent and nondirectional manner, except for short-term increases after Hurricanes Hugo and Georges, which modified habitat structure, followed by decreases to predisturbance levels (4) (figure S3B of ref. 1). Although prehurricane data exist for all 4 of Woolbright's (4) plots, Lister and Garcia (1) do not include these data (figure S3A, C, or D of ref. 1). Stewart's (5) data used by Lister and Garcia are consistent with this phenomenon [i.e., higher numbers after Hurricane David (1979)], followed by a decline to the typical range observed as recently as August 2017.

Lister and Garcia (1) do not consider the effects of changing forest structure following Hurricane Hugo (1989), which inflated avian captures rates at the beginning of the sampling period (6, 7). Their conclusion that the abundance of the insectivorous Puerto Rican tody (*Todus mexicanus*) declined by 90% is not supported by mist-netting data (capture rates from 1980 are similar to those from 2005) or point-count data from the same period (figures 9–11 of Supplementary Materials).

We found no evidence to support the conjecture that food webs are collapsing at LUQ as a result of warming. The narrow focus on temperature-related aspects of climate change as the causative agent does not address the multiple disturbances (e.g., hurricanes and droughts) that affect the forest (8).

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## SUPPLEMENTARY MATERIALS

### LONG-TERM POPULATION TRENDS IN EL YUNQUE NATIONAL FOREST (LUQUILLO EXPERIMENTAL FOREST) DO NOT PROVIDE EVIDENCE FOR DECLINES WITH INCREASING TEMPERATURE OR THE COLLAPSE OF FOOD WEBS

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#### INTRODUCTION

We describe significant concerns related to data selection and transformation, or to the interpretation of trends related to time or temperature for walkingsticks, canopy arthropods, frogs, and birds as published by Lister and Garcia (2018; hereafter L&G). We cannot confidently identify the climatic or abundance data from El Verde that were used by L&G. In some cases, data manipulations were not described explicitly or justifiable. In other cases, the rationale for selection of temporal data for inclusion or exclusion were not apparent. Moreover, errors may have been introduced into the data that compromise its interpretation. Most importantly, L&G failed to consider the effects of disturbance and secondary succession on the abundance of animals in the Luquillo Experimental Forest of Puerto Rico. Short-term responses to cyclonic disturbances, and trajectories of abiotic and biotic characteristics during post-hurricane succession, play a dominant role in modulating variation in abundance of animals in the Luquillo Experimental Forest (see Walker et al. 1991, 1996; Brokaw et al. 2012). Thus, we contend that the role of warming or the suggestion of food web collapse by L&G are oversimplified or unfounded for this tropical forest ecosystem.

#### CLIMATE

**Data concerns.**—Temperature data at El Verde for the time frame discussed by L&G resides in two different sets of data and metadata files, one from 1975 to 1992 (<https://luq.lter.network/data/luqmetadata181>) and one from 1992 to present (<https://luq.lter.network/data/luqmetadata16>). Gaps in temperature records from 1975-1992 were filled by extrapolating from other stations or from other years. Critically, instrument failure in the weather station at El Verde led to underestimates of maximum temperature from 1988-1992. The instrument was replaced in 1992, the housing was rebuilt, and the station was moved. Subsequent measurements recorded maximum temperatures 2 °C higher than at the original instrument. An adjustment was provisionally applied to measurements from the new instrument until 1997; the adjustment was discontinued because the methodology could not be validated for accuracy. Since 26 March 2014, data available to the public from the second instrument do not include an adjustment for any period, and the metadata (<https://luq.lter.network/data/luqmetadata16>) warn users that the two available data sets (1975 to 1992 and 1992-present) should not be treated as a continuous record. The best long-term record of maximum temperature from eastern Puerto Rico is from the National Weather Service station in Fajardo. A 62-yr record from that station shows a small ( $0.024^{\circ}\text{C yr}^{-1}$ ) but significant increase in annual maximum temperature (Greenland and Kittel 2002) that is less than half the increase reported by L&G from their analysis of the El Verde data ( $0.050^{\circ}\text{C yr}^{-1}$ ) or Bisley data ( $0.055^{\circ}\text{C yr}^{-1}$ ).

Moreover, a consistent increase ( $\sim 0.02^{\circ}\text{C}$  per yr) in daily minimum temperature between 2001 and 2013 has been described for sites along elevation gradients in the Luquillo Mountains (Van Beusekom et al. 2015).

L&G do not report the source for the climate data that they used from El Verde or Bisley, although they do for Chamela. We assume that the data for Puerto Rican sites were obtained from the Luquillo LTER online Data Catalog, but requests for confirmation of this assumption to the lead author have not been answered. The temperature data in L&G for El Verde from 1993 onward (see their Figure 1A) mostly correspond to those based on online data, except for the years 1993-1997 (cooler in their graphic, warmer based on the online data). The discrepancy may have arisen because data in L&G included inappropriate adjustments (the algorithm reduced temperature estimates) applied to maximum daily temperatures for 1993-1997 (and perhaps for 1992, as part of that year of data were derived from the first instrument and part of the data were derived from the second instrument). Unfortunately, this cannot be confirmed with confidence (see Figure 1). The temperature data in L&G for Bisley (their Figure 1) may correspond to an online data source for 1993-2010, but L&G report data for Bisley until 2014, which must come from another data set for 2004-2015 (e.g., [https://luq.lter.network/sites/default/files/data/BisMetTwDaily2004-2015\\_0\\_1.csv](https://luq.lter.network/sites/default/files/data/BisMetTwDaily2004-2015_0_1.csv)).

L&G present data (their Figure 1B) documenting a positive relationship between temperature and time at Bisley, and state that the difference between the slopes of the relationship for El Verde and Bisley was not significant. Nonetheless, they did not evaluate the relationship for the more restricted time frame during which data were available for both locations or for the time period associated with abundances of faunal groups examined by them. Moreover, some of the data that they used were incorrect (1993-1997) for El Verde and the temperature data that they used from Bisley came from a number of data sets rather than a single data set. Critically, L&G did not emphasize that temperature data for Bisley were obtained from a sensor mounted above the canopy on a walk-up tower, or that data for El Verde were obtained from a station that was situated 1.5 m above the ground under forest canopy (when present).

***Temporal variation in temperature at El Verde.***—L&G quantify climate change based on the mean of daily maximum temperatures for each year (i.e., their Figure 1A). We calculate this metric independently using data from the online catalog for El Verde (<https://luq.lter.network/data/luqmetadata16>). Clearly, temperature at El Verde significantly declined during both the narrow time frame (1993-2011; Figure 2 upper panel) and the broader time frame (1993-2018; Figure 2 lower panel) of analysis for which we have comparable temperature data and estimates of animal abundance (i.e., walkingstick density [1993-2011], canopy arthropod density [1994-2009], bird abundance from mist nets [1993-2005], frog numbers [1993-2018] and bird abundance from point counts [1993-2017]). Because temperature records from the second climate station at El Verde are only available from the latter three months of 1992, all analyses of variation in abundance with temperature begin in 1993 or later.) In L&G, this cooling trend is visible for the more narrow time period (see their Figure 1A and the red rectangle in Figure 1A) and for the more broad time period at El Verde (see their Figure 1A and Figure 1B), and quite different from that at Bisley (their Figure 1B).

We do not refute that atmospheric temperatures are rising in general, in northeastern Puerto Rico, or in the Luquillo Mountains. Rather, we use the data from El Verde as identified by L&G, to assess possible temperature responses by the fauna at El Verde. Indeed, near ground-level temperatures may

correspond to the thermal environment that is experienced by walkingsticks, frogs, canopy arthropods living in the sub-canopy up to 12 m, and many if not most bird species captured by mist netting or detected through point counts. Using maximum temperature data from El Verde to assess long-term changes in atmospheric temperature (as do L&G) is inappropriate because (1) the two data sets involved do not represent a continuous, long-term set of measurements, (2) the station at El Verde measures temperatures in the shade near ground level rather atmospheric temperature, and (3) measurements at El Verde are influenced by changes in canopy cover.

### WALKINGSTICKS

**Data concerns.**—The data used by L&G to evaluate responses of walkingsticks to time and temperature are uncertain. In the Materials and Methods, L&G stated, “We analyzed data from a census of walkingsticks (*Lamponius portoricensis*) carried out by Willig et al. (24 [2011]) between 1991 and 2014”; however, data were only graphed from 1993 to 2011. The reason for omitting data for walkingsticks from 1991 to 1992 or from 2012 to 2014 was not apparent in the text of L&G. No walkingsticks were captured during the 1991 surveys or during the dry season of 1992 (i.e., abundance = 0), as the population was devastated by Hurricane Hugo in 1989 and had not yet begun to recover to detectable levels (Willig et al. 2011). This, or the undefined nature of  $\ln(0)$ , may have been the rationale of L&G for data exclusion from those years. In addition, L&G state, “To analyze walkingstick abundance through time, we summed all juveniles and adults across seasons and land classes”. Importantly, separate surveys of 40 points on the Luquillo Forest Dynamics Plot (tabonuco forest) were conducted during wet and dry seasons on an annual basis from 1991 through 2011; thereafter surveys were conducted only during wet seasons. The absence of dry season samples may have been the reason for data exclusion from 2012 onward.

An issue not mentioned by L&G was that the number of samples per seasonal survey varied over time (Willig et al. 2011). Each point was sampled once in the dry season of 1991; twice in each season from the wet season of 1991 to the wet season of 1993; three times per season from the dry season of 1994 to the dry season of 1995; and four times per season (except for the dry season of 2003, which was based on two samples) thereafter, until 2012 when surveys were restricted to the wet season and based on four samples per year. This temporal variability in effort could introduce a sampling bias, depending on the metric for estimating abundance. We initially assumed that L&G used the same metric as detailed in Willig et al. (2011) – average number of individuals captured per point – as the basis for estimating cumulative abundance regardless of age group of a walkingstick (adult versus juvenile) or historical land use (intensive logging versus shade coffee plantations versus light and selective logging) associated with a point on the Long-term Forest Dynamics Plot (LFDP). Although not described in their methods, L&G appear to have used the minimum number known to be alive (MNKA) for each age group as the basis for estimating cumulative abundance (i.e., “estimate number” in L&G). The magnitude of a metric based on MNKA is positively correlated with sampling effort, whereas a metric based on the mean abundance will not be biased in that manner, and is more appropriate for temporal analyses in which effort generally increases over time, such as for walkingsticks on the LFDP.

**Long-term trends in abundances.**—In an attempt to replicate the approach of L&G, we conducted analyses based on three time domains (1) 1991 through 2014 (i.e., the time frame stated in their Materials and Methods), (2) 1993 through 2014 (i.e., the time frame for which temperature data were derived from the new instrument), and (3) 1993 through 2011 (i.e., the time frame during which

estimates of walkingstick abundance exist for both the dry and wet seasons, as well as for which temperature data are available from the new instrument). Moreover, we followed the approach of L&G in combining data on walkingsticks for both seasons (when applicable). Nonetheless, based on the text and axis labels in L&G, it is not clear if or how L&G scaled abundance data to arrive at an “estimate number” (although we suspect it was based on MKNA). Consequently, we estimated mean density (number of individuals/ha, where the number of individuals per plot was the mean number of walkingsticks captured over the sampling period) as done in Willig et al. (2011). This resulted in a similar but not identical pattern of “abundance” through time to that illustrated by L&G (compare Figure 3 to their Figure 5C), with the exception of 2011, which appears to be ~0 in their analysis and lower than all other temporal estimates (the plotted point is partially occluded by the X-axis).

As done by L&G, we conducted all analyses as generalized linear models with quasi-Poisson error terms, and used the Ln of walkingstick density as the dependent variable. Nonetheless, we note that it is not necessary or recommended to Ln-transform such data in the context of quasi-Poisson analyses (O’Hara and Kotze 2011), but we do so to adopt the identical approach of L&G. Conclusions from our analyses were similar regardless of time frame. Walkingstick abundance always decreased through time (i.e., best-fit models had a negative slope) and always increased with temperature (i.e., the best-fit models had a positive slope). However, results were not significant for all time frames: abundance significantly decreased with time for 1993-2014 ( $P < 0.001$ ) and for 1993-2011 ( $P = 0.003$ ), but not for 1991-2014 ( $P = 0.432$ ); abundance significantly increased with temperature for 1991-2014 ( $P = 0.007$ ) and for 1993-2014 ( $P = 0.019$ ), but not for 1993-2011 ( $P = 0.109$ ). Regardless of time frame, we find no evidence that walkingstick abundances decreased with increasing temperature (Figure 4). In part, the discrepancy between our results and those of L&G may be related to the estimates for temperature used by L&G.

## CANOPY ARTHROPODS

**Data concerns.**—It is not clear how L&G analyzed the data for canopy arthropods (<https://luq.lter.network/data/luqmetadata96>). Their methods state that they “summed all arthropods sampled each year across taxa, forest type, and tree genera.” In contrast, data that are graphed (Figs. 5A and 5B of L&G) are densities (individuals per gram of foliage collected for a sample). Because branch bagging does not collect a constant foliage volume, especially for tree species with different structural designs and physical arrangements of branches and leaves, arthropod counts vary significantly with foliage mass (Schowalter et al. 2014, 2017). Consequently, arthropod density is an appropriate approach to analyze these data, although we caution that such densities may not be related to overall variation in population sizes because the number of captured individuals is contingent on the amount and types of vegetation in the forest.

Combining canopy arthropod data within each year without regard for the host-tree species from which they were collected is highly problematic. We selected early and late successional tree species, as well as overstory and understory taxa. Our approach does not estimate abundance of canopy arthropods throughout the forest because our sampling does not represent a random or representative assortment of tree species from the LFDP. Because the composition of arthropod assemblages differs significantly among tree species, the origin of samples must be taken into account in analysis. Moreover, the same tree species were not available for sampling during the entire period of study due to the impacts of disturbance and subsequent regeneration of the forest, including turnover of tree species composition associated with Hurricanes Hugo and Georges. Densities of arthropods are host-tree specific; ignoring

the identities of these trees combines data that are not comparable. Regardless, we cannot reproduce the data plotted in L&G (their Figure 5A and 5B). For example, they do not display any total densities > 0.3 individuals per gram of foliage weight, whereas 3 years (i.e., 1995, 2001, and 2002) are characterized by densities > 0.3 individuals per gram of foliage weight when considering only the 10 most abundant arthropod taxa rather than all taxa (Figure 5). Nonetheless, the general trend for arthropod density over time is similar in L&G to that for the cumulative density of the 10 most abundant taxa (Figure 5).

**Long-term trends in abundances.**—L&G assert that data from the Luquillo Experimental Forest reveal a significant temporal decline in density (captures per foliage weight) of canopy arthropods (their Figure 5A), but do not show a significant decline in density with temperature (their Figure 5B). For unknown reasons, L&G introduced quadratic and cubic parameters to obtain a significant model of the relationship between arthropod density and temperature. Regardless, the displayed data do not show a consistent negative response by arthropod density to temperature. Indeed, a complex polynomial model suggests that the rate of change is not monotonic, and contrary to their supposition, arthropod density increased with increasing temperature for most of the temperature range (i.e., temperatures > 26 °C) illustrated by their figure.

L&G claimed that each of the 10 most abundant arthropod taxa exhibited negative trends in abundance (not density) with time. We agree that this likely is true, and a re-analysis of original count data for the ten most abundant taxa corroborates that all declined over time, but only five of them declined significantly over time. Importantly, this result is likely a sampling artefact. More specifically, sample effort declined appreciably over the time period of study, from 4 sample sessions per year during the early 1990s to only 1 sample sessions per year by the late 2000s. As such, any change in counts summed for each year (consistent with their statement of using abundances in both the results and methods) is strongly affected by variation in sampling effort, and not necessarily a response by canopy arthropods to time or temperature.

We evaluated temporal changes in density of the 10 most abundant taxa (Table 1): 5 taxa exhibited decreases in density over time and 5 taxa exhibited increases in density over time, with only 1 response being significant. As a group (cumulative density of all 10 taxa), density did not exhibit a significant temporal decrease (Table 1, Figure 5). In contrast, the density of 8 of 10 taxa increased with increasing temperature. Moreover, the only 2 significant temperature responses were in this direction. Finally, the cumulative density of the 10 most abundant taxa increased with increasing temperature (Table 1, Figure 6). We can find no evidence that canopy arthropods decrease in response to increasing temperatures at El Verde. (Note: we restricted analyses to data available for the new weather station instrument to avoid combining temperature data that are not compatible.)

To further consider the potential for temperature to influence the density of canopy arthropods, we conducted analyses that controlled for the species identity of host trees. Separately for each tree species, we evaluated the response of arthropod density (all species combined, about 170 taxa) to time and temperature (Table 2). Arthropod density on 2 of the 6 tree species decreased significantly over time (trends were not significant on the other 4 tree species). In contrast, arthropod density on 2 of the 6 tree species increased with increasing temperature (trends were not significant on the other 4 tree species). We find no evidence that temperature is driving declines in arthropod abundances.

## COQUIS

**Data concerns.**—Long-term census data concerning coqui (*Eleutherodactylus coqui*) populations derive from four 400 m<sup>2</sup> study plots in El Yunque National Forest: two in the Bisley Watersheds (1988-2011) and two at El Verde (1987-2017). Standard census methods for obtaining estimates appear in Woolbright (2005). In general, the total number of unique adults captured during a 4-night census period based on mark-recapture methodologies are the most reliable indicator of adult population size (Woolbright 2005), and L&G seem to have used this approach for quantifying abundance.

Although L&G cite Woolbright (1996) as one of the sources of their data, they refer to the range of years as 1987 to 1997, so the source and identity of data for the years (1996-1997) not included in Woolbright (1996) are not clear. L&G also state that Bisley plot data have not been reported previously, when in fact, such data are included in Woolbright (1996). Moreover, L&G state that they removed one data point from one of the El Verde plots in 1995 because abundance "increased from 29 to 236 and returned to 45 individuals in the next census". Both 29 and 45 individuals correspond to typical adult counts from a single plot. Nonetheless, we do not see those data in the 1995 data reported for that plot in Woolbright (1996). Moreover, we cannot find the count of 236 individuals in the data for adults, and it likely is an estimate that includes juveniles. In short, we are unable to determine the full identity of the data that have been used in L&G, and we cannot corroborate the accuracy of some of the selected data for El Verde.

L&G report coqui abundances from 1979 to 1993 (their Figure 7A) and cite the source as data from an activity transect study (Stewart 1995). The methodology of her study was not that same as that of Woolbright (2005), so both sets of data must be compared with caution. Stewart (1995) reported the maximum number of frogs counted on any night during three consecutive nights (individuals were not marked). In contrast, Woolbright (2005) marked individual frogs, and reported the total number of such uniquely marked frogs collected over four consecutive nights. Nightly numbers are quite variable depending largely on weather conditions, and the maximum number is a function of the number of sampling nights by both methods. Moreover, it appears that L&G included juvenile counts from Stewart (1995) in their estimates. Juveniles have high mortality rates and their activity is affected greatly by dry weather. In addition, juvenile counts are not good indicators of population status or trajectories due to their non-reproductive status and high mortality.

Finally, we cannot identify the source(s) of the large number of data points that appear in L&G for temporal trends in abundance of coquis at El Verde (their Figure S3B). The segmented regression approach effectively characterized three periods of changing abundance (before Hurricane Hugo; short-term post-Hugo succession, and long-term post-Hugo succession), but the explicit rationale for the exact segmented periods was not provided in L&G.

**Long-term trends in abundances.**—We combine unpublished data with those in the LTER data repository (Table 3) to explore 30 year trends (1987-2017) in abundance of adult coquis at two plots (Sonadora-Old and Sonadora-New) at El Verde and two plots (Forest Control, Stream 2) at Bisley (Figure 7). A number of salient features characterize temporal trends at El Verde and Bisley. First, pre-Hugo estimates were moderately variable, with little evidence of a directional change in abundance. Second, over the short term (1 year), abundances drastically increased (blue shaded area in Figure 7) after Hurricane Hugo. Third, after this initial increase, longer term (1-9 years post disturbance) declines in abundance occurred until estimates were within the range seen prior to Hurricane Hugo (yellow shaded



areas of Figure 7). Fourth, short term responses to Hurricane Georges (green shaded area in Figure 7) were variable with at best modest indications of an increase in abundance, perhaps because Hurricane Georges caused less canopy opening and less litter deposition than did Hurricane Hugo (Ostertag et al. 2003, Canham et al. 2010). Fifth, variation in abundance after Hurricane Georges (2-18 years at El Verde, 2-11 years at Bisley) was generally within the range of variability seen prior to Hurricane Hugo (yellow shaded areas of Figure 7).

Pending a comprehensive statistical analysis of data, we generally followed the approach of L&G. More specifically, we conducted statistical analyses as generalized linear models with quasi-Poisson error terms, and used the Ln of coqui numbers as the dependent variable. We did so for each of three time periods: before Hurricane Hugo (red A in Figure 7), one year after Hurricane Hugo but before Hurricane Georges (red B in Figure 7), and one year after Hurricane Georges (red C in Figure 7). Results were similar at Bisley and El Verde: (1) no significant temporal changes in abundance prior to Hurricane Hugo (El Verde:  $B_1 = -0.050$ ,  $P = 0.154$ ; Bisley:  $B_1 = -0.085$ ,  $P = 0.239$ ); (2) significant temporal decreases in abundance from one year after Hurricane Hugo to before Hurricane Georges (El Verde:  $B_1 = -0.0410$ ,  $P < 0.001$ ; Bisley:  $B_1 = -0.029$ ,  $P = 0.006$ ), and (3) no significant temporal changes in abundance from one year after Hurricane Georges to 2018 at El Verde ( $B_1 = 0.000$ ,  $P = 0.898$ ) or to 2011 at Bisley ( $B_1 = 0.001$ ,  $P = 0.869$ ). Taken together, these data indicate that temporal trends in abundance correspond to considerations of disturbance and response in hurricane-mediated systems, such as those in the Luquillo Mountains of Puerto Rico. Moreover, the only evidence of a declining temporal trend in abundance occurs after Hurricane Hugo, and even in this case, abundances return to estimates within the range of those prior to Hurricane Hugo or after Hurricane Georges. For the period of 1993-2017, we find no evidence that increasing temperature leads to declines in frog abundance at El Verde. Indeed, frog abundance statistically increased with increasing annual mean maximum daily temperature (Figure 8). That similar patterns of temporal variation in abundance characterized El Verde (where temperature is decreasing close to ground level) and Bisley (where temperature is increasing at canopy level) suggests that neither measure is causative, but that each is correlated with time after disturbance from Hurricane Hugo. Thus, we do not see a strong signal of warming or declines in abundance for frogs, but instead see clear and parallel disturbance dynamics at El Verde and Bisley, likely related to hurricane-induced alterations in habitat structure (Stewart and Pough 1983, Woolbright 1991, 1996).

## BIRDS

**Data concerns.**—L&G analyzed mist-netting data from El Verde covering the period 1990-2005 (not 2015 as L&G state). They downloaded data (LUQ Data Set 173; DOI 10.6073/pasta/193494ce39da414e09c97f9384e05ce2) from the online Luquillo LTER Data Catalog, which provides data and metadata for all data sets. L&G analyzed the relationship between the total number of birds captured annually and both time and temperature (their Figure 7C and 7D). However, they did not correct for annual variation in sampling effort, which ranged from 382.5 to 995.0 net-hours over the course of the netting study. The data for number of captures (their Figure 7C) does not match data from Data Set 173, even accounting for their exclusion of captures of Ruddy Quail-Doves (*Geotrygon montana*), suggesting that additional undescribed manipulations may have been performed on the data. Moreover, they incorrectly describe the remaining species as insectivores. In fact, most of these species are omnivores, with the proportion of invertebrates in their diet ranging from 0 to 59.7% (Waide 1996). The only true insectivore in the netting samples is the Puerto Rican Tody (*Todus mexicanus*). L&G's regression of number of captures on temperature suffers from the same problems

with faulty maximum temperature data as discussed for other organisms. Moreover, for the period of analysis, number of captures declines with decreasing temperature in contrast to results from L&G's analysis. The cumulative effect of these data concerns is to cast doubt on the results of L&G's analysis.

L&G also examine the relationship between mist net catch rate relative to the Ruddy Quail-Dove and the proportion of invertebrates in the diets of six species. The Ruddy Quail-Dove was chosen as a baseline because it is "a granivore that showed no decrease in abundance between 1990 and 2005" (Supporting Information in their Figure S4). It is unclear from L&G how the calculation of relative loss of catch rate was made, and we have been unable to replicate their analysis. Moreover, the choice of the Ruddy Quail-Dove as a baseline is questionable. Quail-Doves underwent a very significant decline in capture rate between 1980 (Waide 1991) and 1990 (3.15 vs. 0.11 captures per 100 net-hours), probably as a result of Hurricane Hugo in 1989. Only one Quail-Dove was captured in 1990, leaving very little room for further decline. Instead, Quail-Dove numbers increased greatly over time (4.34 captures per 100 net-hours) until Hurricane Georges in 1998 reduced them to a single capture the following year.

**Long-term trends in abundances.**—L&G argue that their analysis of mist-netting data shows a long-term decline in abundance that they attribute to the effects of increasing temperature. However, correcting for the effects of variation in sampling effort substantially alters the shape of the relationship between capture rate and time (Figure 9, upper panel). After a peak in capture rate in 1990, within a year of the impact of Hurricane Hugo, capture rates declined and remained steady between 6-10 captures per 100 net-hours. If anything, there is an increase in capture rate beginning in 1996, but the subsequent impact of Hurricane Georges complicates the interpretation of that observation. Hence, these data do not show a consistent long-term decrease in abundance. The peak in 1990 and subsequent variation is attributable to changes in avian foraging behavior resulting from the wholesale reorganization of canopy structure (Waide 1991, Wunderle 1995), and the details of the mist-netting data bear this out. For example, capture rates of 11 of 13 species increased after the hurricane by as much as 12-fold. Increases in post-hurricane capture rates have been reported by other investigators in Yucatan (Lynch 1991) and at El Verde (Wunderle 1995). Regardless of temporal trends, capture rates of all birds are not statistically related to variation in temperature (Figure 10, upper panel).

L&G posit that declines in the abundance of insectivores like the Puerto Rican Tody support their thesis that warming is reducing insect abundance with cascading effects on the food web. Capture rates of Todies do decline between Hurricanes Hugo and Georges (but only at a more lenient  $\alpha$ -level of 0.10), but rebound to above mean pre-hurricane values by 2005 (Figure 9, lower panel). Regardless of temporal trends, capture rates of the Puerto Rican Tody are not statistically related to temperature (Figure 10, lower panel). Moreover, long-term data on Tody abundance measured by counts at 40 points in the Luquillo Forest Dynamics Plot (LUQ LTER Data Set 23; DOI [10.6073/pasta/91e6302e743bac1e3e32781b869ce3d9](https://doi.org/10.6073/pasta/91e6302e743bac1e3e32781b869ce3d9)) show no evidence of a precipitous decline (in contrast to the contention of L&G) and in fact do not vary significantly with time over a 28 year period (Figure 11, upper panel). These long-term data show substantial annual variation in Tody abundance, but they do not support L&G's claim of a 90% reduction in the abundance of this species. Moreover, abundance as estimated through point counts does not vary statistically with temperature, regardless of temporal patterns (Figure 11, lower panel).

No direct evidence in L&G or in our data and analyses suggest a long-term decline in avian abundance attributable to reduced numbers of arthropods as a result of increasing temperature. Habitat

restructuring as a result of Hurricane Hugo is a more reasonable explanation for the decline in capture rates between 1990 and 1998. Moreover, long-term records based on point counts indicate that populations of the insectivorous Tody, although variable, have not exhibited a directional change during the last 28 years.

## CONCLUSIONS

At El Verde, we have documented that faunal abundance is unrelated to temperature (i.e., walkingsticks, birds in general, or Puerto Rican Tody in particular) or is positively associated with temperature (i.e., canopy arthropods and frogs). Thus, for these taxa in this location, there is no evidence for warming, as reflected in annual mean daily maximum temperature, effecting any declines in abundance that might lead to food web collapse. Moreover, temporal variations in abundance, including increases and decreases, are explicable in the context of hurricane-induced disturbances and subsequent secondary succession. Indeed, we have demonstrated here and elsewhere that much of the temporal variation in the abundances or densities of walkingsticks, canopy arthropods, frogs, and birds is likely initiated by and related to hurricane-induced disturbances (e.g., Walker et al. 1991, 1996, Brokaw et al. 2012). Unfortunately, effects of hurricanes on temporal trajectories of faunal abundances were not considered in a comprehensive way by L&G. Indeed, temporal variation in metrics of abundance for each of the four faunal groups represents decadal recovery periods following Hurricanes Hugo (1989) or following Hurricane Georges (1998). For the two vertebrate groups (frogs, and birds), short-term responses to hurricanes (12 months) are characterized by elevated abundances or densities, which subsequently decline as the forest regrows, eventually attaining values that are similar to those before Hurricane impacts. In contrast, the short-term response of walkingsticks to Hurricane Hugo was a drastic reduction in density to undetectable numbers that persisted for a few years before rebounding to levels that were indistinguishable to those before 1989. Nonetheless, walkingstick density declined immediately before the impact of Hurricane Georges, and remained considerably below levels prior to Hurricane Hugo (Willig et al. 2011). Beginning five years after Hurricane Hugo (1994), abundances of canopy arthropods on a mix of host trees fluctuated over time, but failed to evince any simple temporal trend.

Short-term responses to cyclonic disturbances, and trajectories of abiotic and biotic characteristics during post-hurricane succession (see Brokaw et al. 2012, Shiels et al. 2014), play a dominant role in modulating variation in abundance of animals in the Luquillo Experimental Forest. We contend that the role of warming or the suggestion of food web collapse by L&G are oversimplified or unfounded, respectively, in this tropical forest ecosystem. In the Luquillo Experimental Forest, the resistance and resilience of the fauna to press (temperature change) or pulse (hurricanes) disturbances may arise because of the evolutionary history of a biota that has been subjected for millennia to a hurricane-dominated disturbance regime that selects for considerable tolerance to environmental fluctuation. Nonetheless, it is critical to continue long-term monitoring of population, community, and ecosystem dynamics, especially because of the complex interplay between press and pulse disturbances, the possibility of tipping points, and the need to evaluate sufficient empirical evidence to make sound environmental diagnoses and prognoses that can inform management and conservation action.

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Table 1. Results of simple linear regressions conducted separately on the density (individuals per gram of foliage) of each of the 10 most abundant species of canopy arthropod as well as on the cumulative densities of these 10 species to evaluate responses to temperature or time. When density of an arthropod taxon was significant, it increased with increasing temperature ( $B_1 > 0$ ). In contrast to the results of L&G, we find no evidence that the density of any of the 10 most abundant species of canopy arthropod individually or in aggregate declined in response to temperature or that they exhibit consistent temporal responses.  $B_0$  = intercept;  $B_1$  = slope; significant results ( $P \leq 0.05$ ) are bold.

Arthropod taxon	Temperature				Year			
	$B_0$	$B_1$	P	$R^2$	$B_0$	$B_1$	P	$R^2$
<i>Wasmannia auropunctata</i>	-1.637	0.062	0.114	0.211	10.062	-0.005	0.373	0.073
<i>Ceroplastes rubens</i>	-0.118	0.005	0.549	0.034	1.222	1.222	0.604	0.025
<i>Cyrtoxipha gundlachi</i>	0.156	-0.004	0.438	0.056	-2.377	0.001	0.100	0.227
<i>Vinsonia stellata</i>	<b>-0.287</b>	<b>0.011</b>	<b>0.003</b>	<b>0.555</b>	2.101	-0.001	0.068	0.271
<i>Coccus acutissimus</i>	-0.039	0.002	0.903	0.001	0.982	0.000	0.839	0.004
Pseudococcid scale insect	1.005	-0.032	0.879	0.002	-12.570	0.006	0.827	0.005
Psocoptera spp.	<b>-0.853</b>	<b>0.032</b>	<b>&lt; 0.001</b>	<b>0.791</b>	<b>8.648</b>	<b>-0.004</b>	<b>&lt; 0.001</b>	<b>0.761</b>
Collembola spp.	-0.059	0.003	0.758	0.009	2.413	-0.001	0.336	0.084
<i>Protopulvinaria pyriformis</i>	-0.141	0.005	0.085	0.245	1.046	-0.001	0.246	0.120
<i>Lyssomanes portoricensis</i>	-0.049	0.002	0.120	0.205	0.657	0.000	0.085	0.245
Cumulative density	-2.959	0.117	<b>0.021</b>	<b>0.397</b>	23.646	-0.012	0.110	0.215

Table 2. Results of simple linear regressions evaluating responses of canopy arthropod density (individuals per gram of foliage) to temperature (mean maximum daily temperature) and time at El Verde Field station in Puerto Rico. Analyses were performed separately for each of 6 host tree species. Arthropod density decreased over time on two species of host tree ( $B_1 < 0$ ), but increased with temperature on two species of host tree ( $B_1 > 0$ ).  $B_0$  = intercept;  $B_1$  = slope; significant results ( $P \leq 0.05$ ) are bold.

Host tree species	Temperature				Year			
	$B_0$	$B_1$	P	$R^2$	$B_0$	$B_1$	P	$R^2$
<i>Casearia arborea</i>	-8.971	0.370	0.059	0.341	<b>170.86</b>	<b>-0.085</b>	<b>0.004</b>	<b>0.615</b>
<i>Cecropia schreberiana</i>	9.048	-2.828	0.890	0.002	-108.67	0.547	0.844	0.004
<i>Dacryodes excelsa</i>	-2.172	0.099	0.485	0.045	23.21	-0.011	0.556	0.032
<i>Manilkara bidentata</i>	<b>-6.772</b>	<b>0.281</b>	<b>0.016</b>	<b>0.423</b>	<b>85.39</b>	<b>-0.042</b>	<b>0.006</b>	<b>0.517</b>
<i>Prestoea acuminata</i>	<b>-15.399</b>	<b>0.597</b>	<b>0.045</b>	<b>0.319</b>	89.99	-0.045	0.305	0.095
<i>Sloanea berteriana</i>	2.311	-0.053	0.424	0.059	-6.71	0.004	0.678	0.016

Table 3. Number of uniquely marked adult *Eleutherodactylus coqui* encountered during a 4-night census of each plot, during each field season (month and year). Each night consisted of a 1-hour time-constrained search of the 20 × 20 m plot. Search time excluded handling time when a frog was captured. Missing values indicate that the plot was not censused that field season.

Field season		El Verde		Bisley	
Year	Month	Sonadora west old plot	Sonadora west new plot	Forest control plot	Stream 2 plot
1987	January	55	36		
1987	July	33	22		
1988	January	38	23		
1988	June	29	31	33	35
1989	January	46	36	41	38
1989	June	19	19	22	27
1989	October	24	24	37	23
1990	January	28	19	40	28
1990	March	44	21	42	32
1990	June	77	41	42	36
1990	August	55	45		
1990	October	158	146		
1990	December	138	108		
1991	February	114	108		
1991	March	66	61	135	118
1991	July	79	114		
1992	January	82	83	109	61
1992	June	114	135	141	67
1993	January	96	106	101	72
1993	June	80	81	98	54
1994	January	87	64	78	39
1994	July	58	66	86	32
1994	October	76	48	73	25
1995	January	30	39	62	26
1995	June	43	32	36	17
1996	January	79	56	40	41
1996	June	46	34	22	22
1997	January	53	40	31	16
1997	June	39	32	32	6
1997	December	46	27	35	14
1998	June	45	26	52	16
1998	November	57	49	64	57



Table 3. Continued.

Field season		El Verde		Bisley	
Year	Month	Sonadora west old plot	Sonadora west new plot	Forest control plot	Stream 2 plot
1999	January	60	60	48	48
1999	March	30	32	20	36
1999	August	77	92	93	51
2000	January	39	42	46	31
2000	August	37	22	48	40
2001	August	81	40	13	43
2002	August	52	36	40	41
2005	March	53	18	19	20
2006	May	42	35	43	20
2007	January	88	60	36	37
2009	May	20	19		
2009	December	47	42	38	25
2010	May	38	34	61	38
2010	December	48	45	30	32
2011	May	40	31	37	37
2011	September	47	39		
2011	October	64	58		
2011	December	53	56		
2012	January	19	35		
2012	March	49	37		
2014	December	45	43		
2015	May	39	29		
2015	September	50	41		
2015	November	46	45		
2016	April	38	40		
2016	September	63	43		
2017	February	30	21		
2017	May	54	38		
2017	September	54	35		

Figure 1

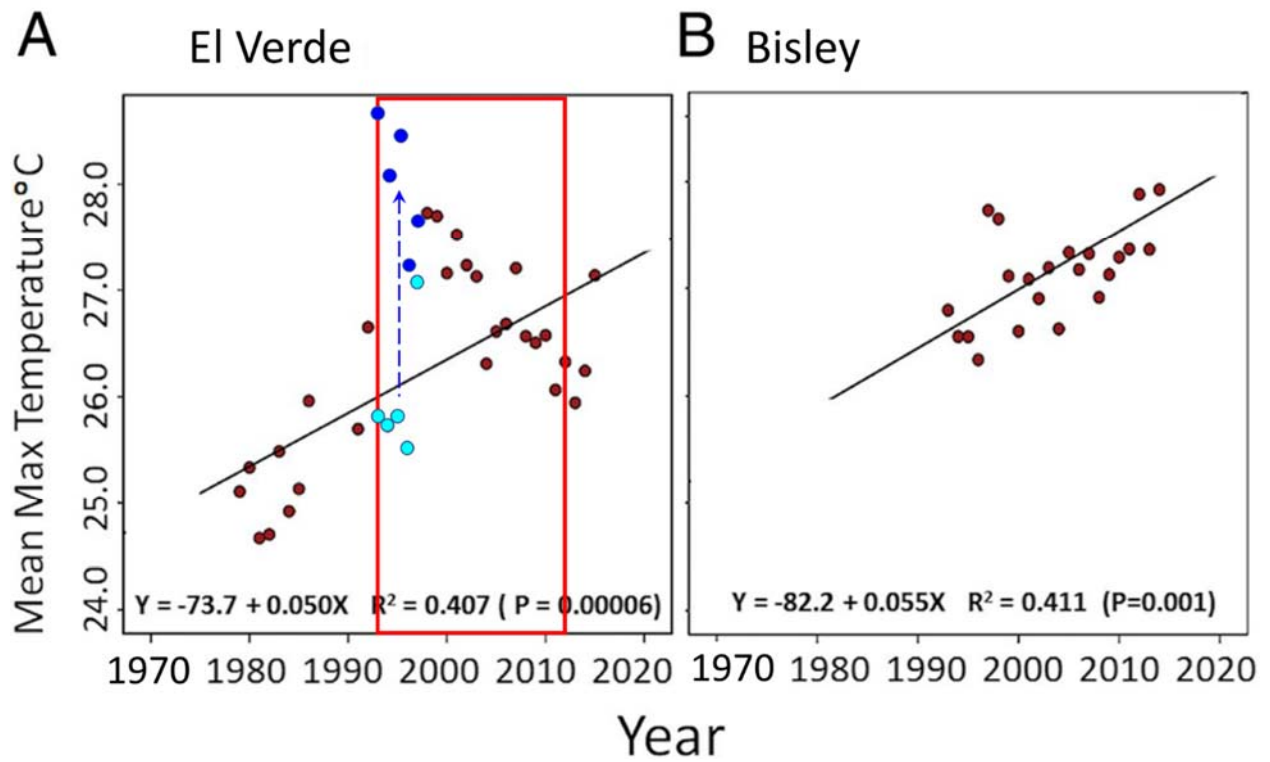


Figure 1. Temporal trends in temperature at El Verde (A) and Bisley (B) from L&G (with some additions and corrections). The red rectangle delimits the time frame used for analysis of walkingstick abundances at El Verde. Importantly, temperature data for 1993-1997 (points highlighted in light blue) at El Verde may reflect an erroneous adjustment that was not applied to subsequent data. Indeed, the online data for El Verde contain higher temperatures for those five years (dark blue points). After considering these issues, it is clear that temperature cooled at El Verde during the time period for which walkingstick data were analyzed.

Figure 2

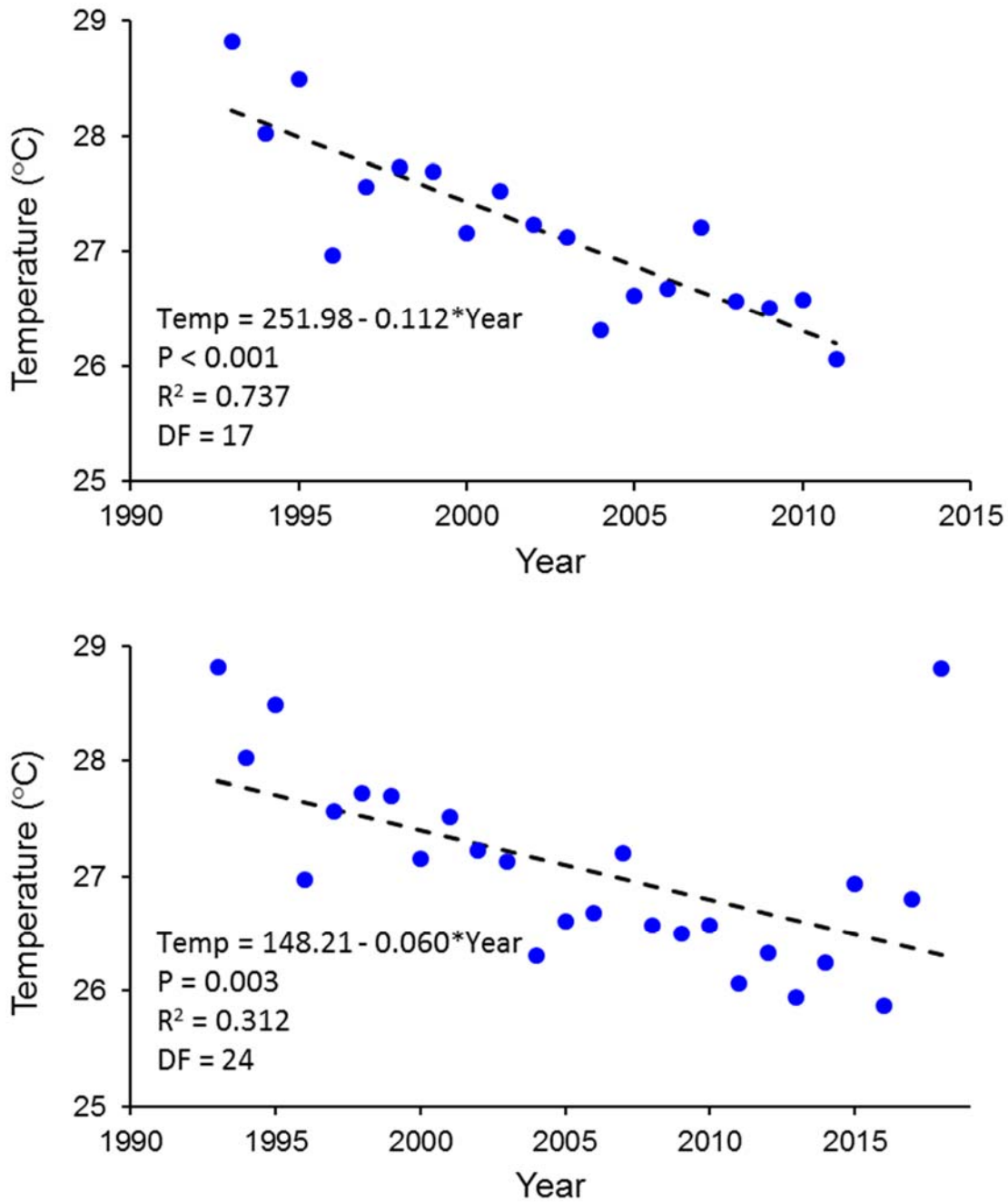


Figure 2. The relationship between temperature (mean maximum daily temperature) and year for El Verde based on simple linear regressions. The relationship was evaluated for 2 timeframes: a more narrow temporal window (1993 to 2011) that corresponds to analyses of walkingstick density, canopy arthropod density, and bird density; and a more broad window (1993 to 2018) that corresponds to analyses of frog abundance and bird point counts. All temperature data are from the newer weather station that was installed in late 1992 in the forest understory. These highly significant cooling trends during this period contrasts with the conclusion of L&G and likely result from the regeneration of the forest after Hurricane Hugo. The increase in temperature in 2018 reflects the effects of Hurricane Maria, which removed much of the forest canopy.

Figure 3

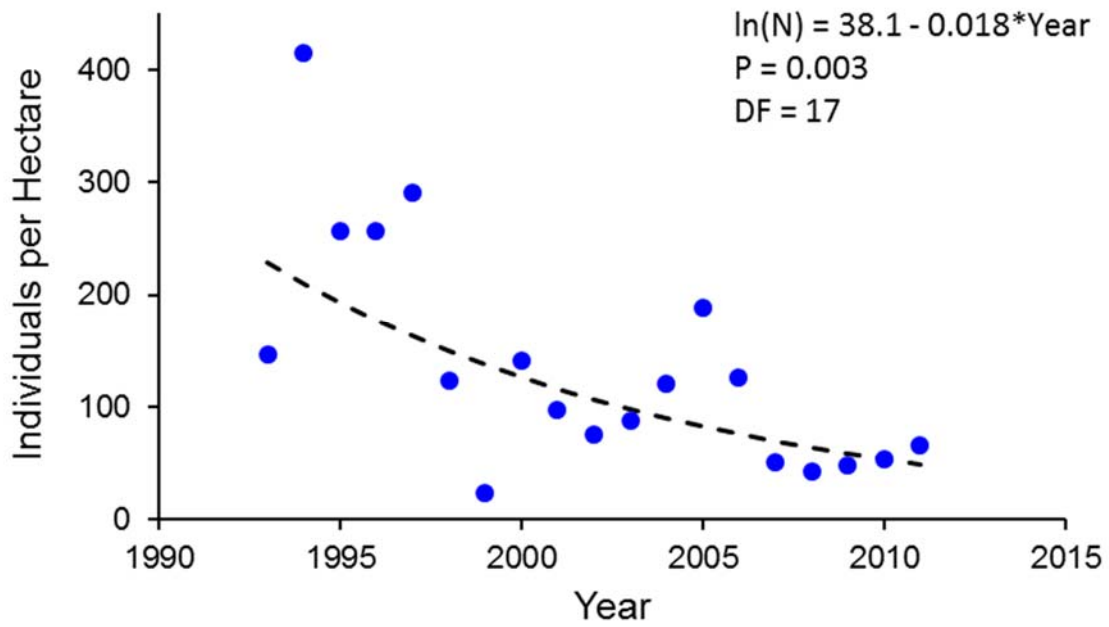


Figure 3. The relationship between walkingstick density (ln-transformed) and year for El Verde based on a quasi-Poisson model. The relationship was evaluated for 1993 to 2011, the years for which (1) wet and dry season abundances of walkingsticks are available and (2) temperature data derive from the same climate instrument. The long-term decrease in abundance is similar to that of L&G.

Figure 4

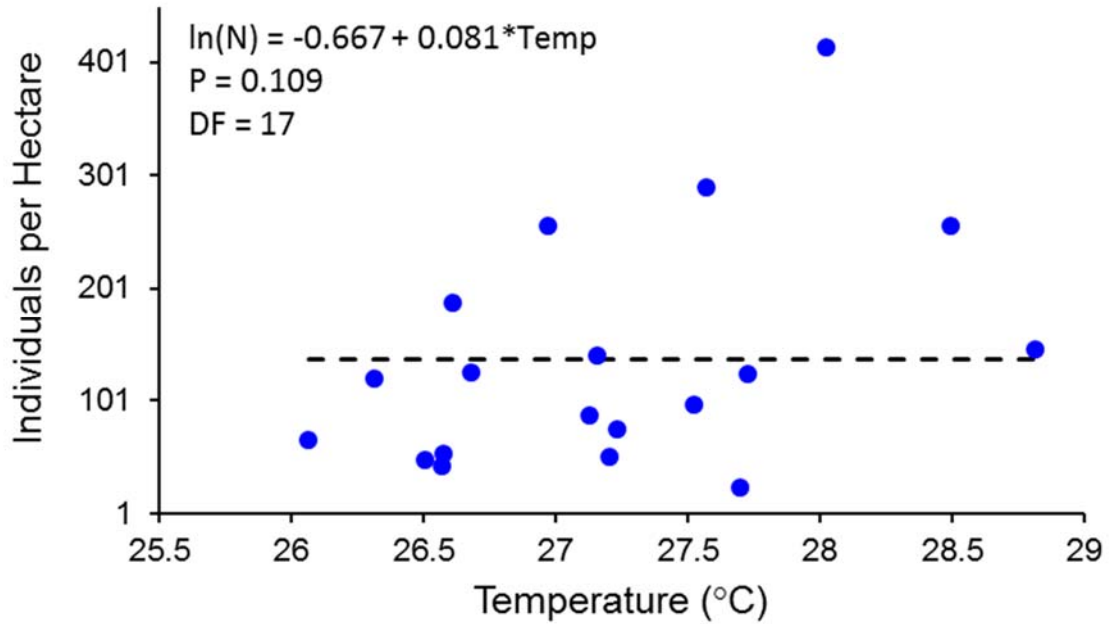


Figure 4. The relationship between walkingstick density (ln-transformed) and temperature (mean maximum daily temperature) for El Verde based on a quasi-Poisson model. The relationship was evaluated for 1993 to 2011, the years for which (1) wet and dry season abundances of walkingsticks are available and (2) temperature data derive from the same climate instrument. In stark contrast to the assessment by L&G, variation in the abundances of walkingsticks is not statistically related to variation in temperature at El Verde (and the empirical slope is positive rather than negative, as in L&G).

Figure 5

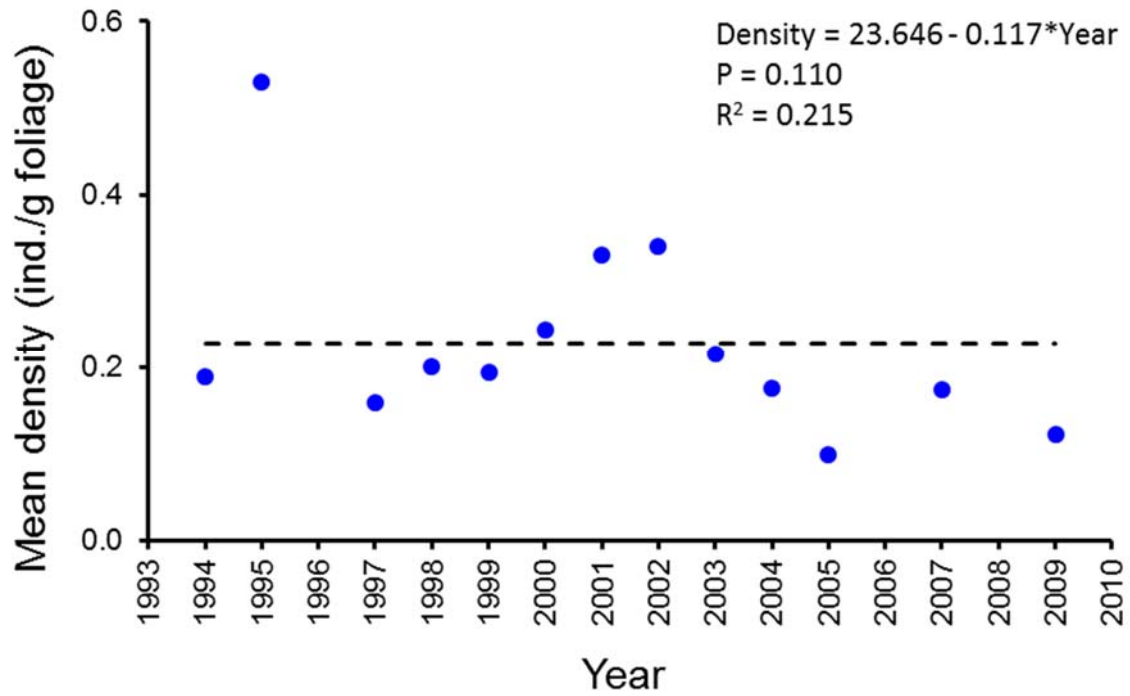


Figure 5. The relationship between canopy arthropod density (cumulative density of the 10 most abundant taxa based on gram of foliage mass) and year based on a simple linear regression (Table 1). This empirical trend is similar to that in L&G, but does not represent a significant decrease over time ( $P = 0.110$ ,  $R^2 = 0.215$ ) as reported in L&G.

Figure 6

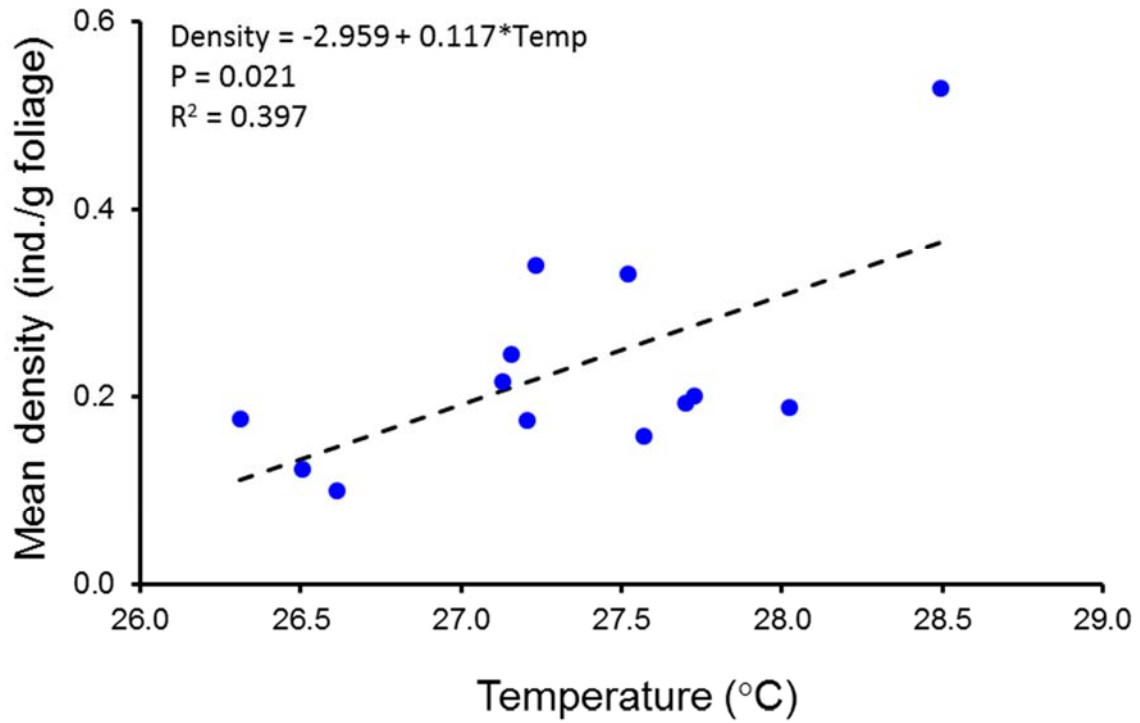


Figure 6. The relationship between canopy arthropod density (cumulative density of the 10 most abundant taxa based on a gram of foliage mass) and temperature based on a simple linear regression (Table 1). In contrast to the trend reported in L&G, arthropod densities increased with increasing temperature between 1994 and 2009. ( $P = 0.021$ ,  $R^2 = 0.397$ ).

Figure 7

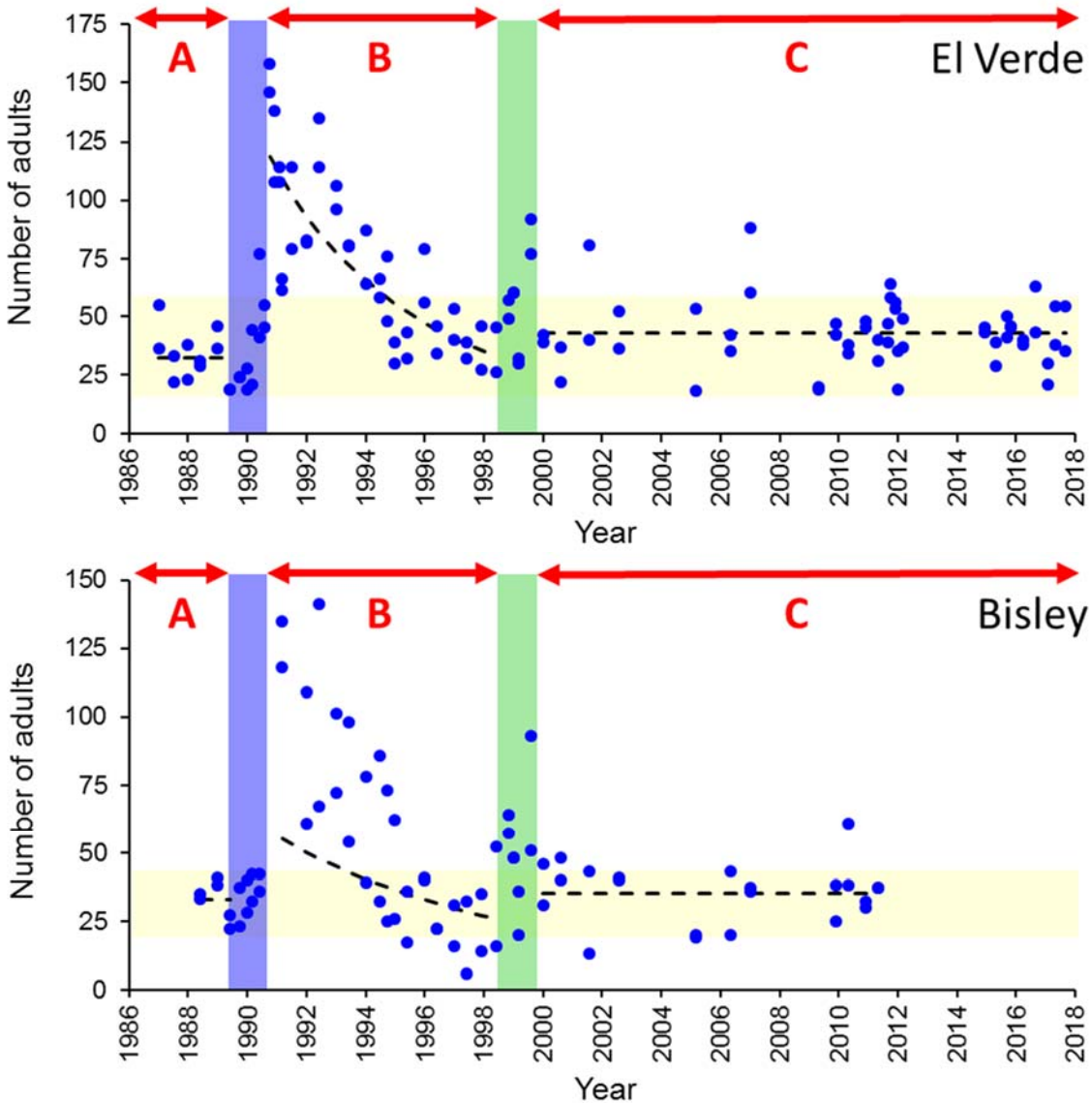


Figure 7. Long term trends of adult *Eleutherodactylus coqui* in the Sonadora Watershed at El Verde and at the Bisley Watersheds. Vertical shaded regions indicate the immediate response (i.e., 12 months) of coqui after Hurricanes Hugo (blue shaded areas) and Georges (green shaded areas) during the falls of 1989 and 1998, respectively. The horizontal shaded regions in yellow indicate the ranges in abundance before Hurricane Hugo. Time periods are indicated by red arrows: A, pre-Hurricane Hugo; B, post-Hurricane Hugo; C, post-Hurricane Georges. No significant temporal variation characterized periods before Hurricane Hugo (El Verde:  $B_1 = -0.050$ ,  $P = 0.154$ ; Bisley:  $B_1 = -0.085$ ,  $P = 0.239$ ) or after Hurricane Georges (El Verde:  $B_1 = 0.0003$ ,  $P = 0.898$ ; Bisley:  $B_1 = 0.001$ ,  $P = 0.869$ ). In contrast, secondary succession after Hurricane Hugo, but before Hurricane Georges, was characterized by significant temporal declines in abundance at El Verde and Bisley (El Verde:  $B_1 = -0.041$ ,  $P < 0.001$ ; Bisley:  $B_1 = -0.029$ ,  $P = 0.006$ ). Analyses were conducted separately for each combination of location and time period (A, B, and C) using a quasi-Poisson model and ln-transformed counts of adult *Eleutherodactylus coqui*. As multiple surveys were conducted each year, we estimated time using fractional years based on months (i.e., to the nearest 1/12<sup>th</sup> year).



Figure 8

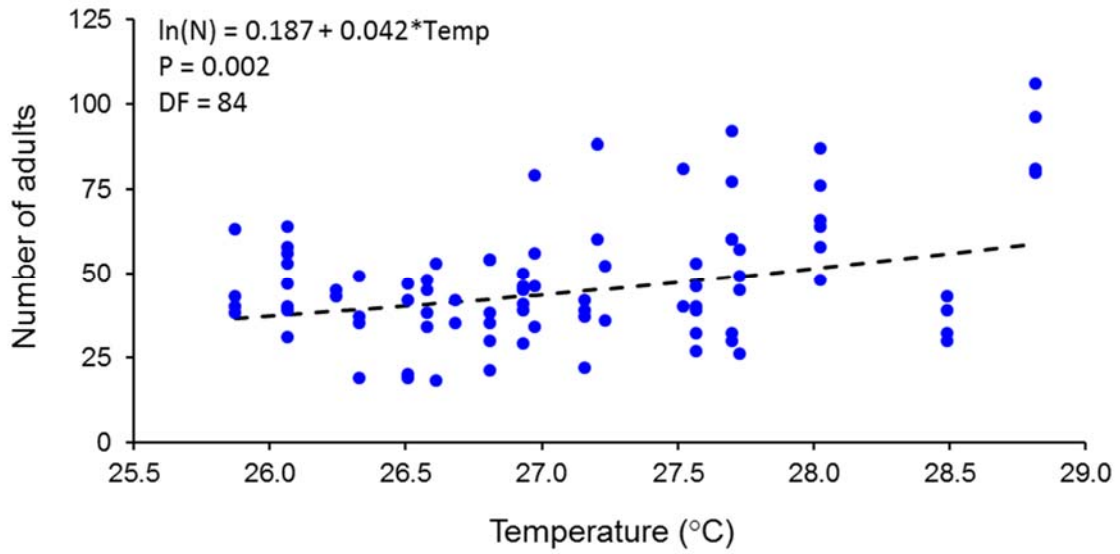


Figure 8. The relationship between the number of adult *Eleutherodactylus coqui* (ln-transformed) and temperature based on a quasi-Poisson model. In contrast to the trend reported in L&G, frog densities increased with increasing temperature between 1994 and 2009. ( $B_1 = 0.042$ ,  $P = 0.002$ ).

Figure 9

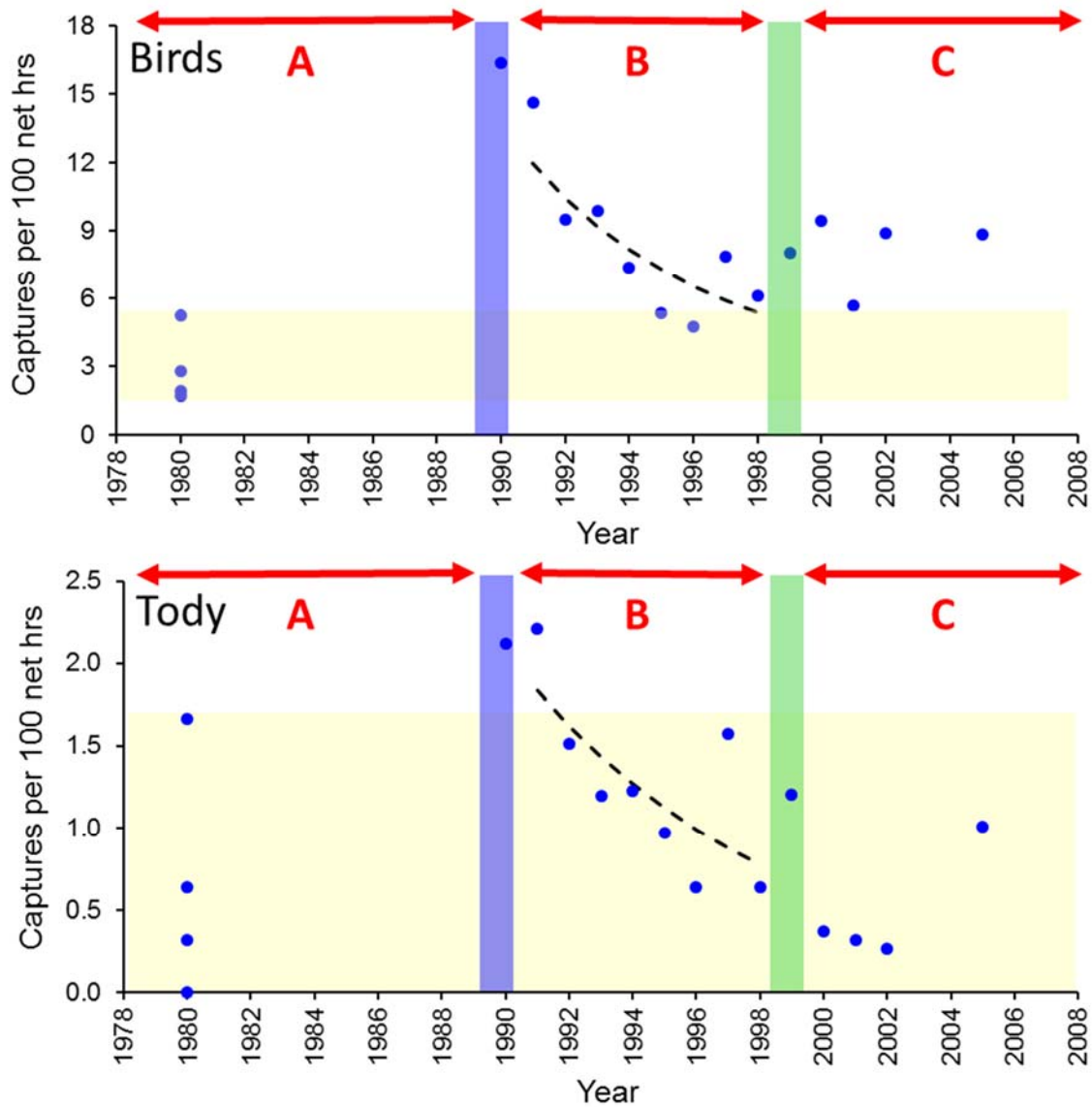


Figure 9. Long-term temporal trends in abundance (captures per 100 mist net hours) for all birds except for the Ruddy Quail-Dove (upper panel) and for the Puerto Rican Tody (lower panel) at El Verde from 1980 to 2005. Shaded vertical regions indicate the immediate response (i.e., 12 months) after Hurricanes Hugo (blue shaded areas) and Georges (green shaded areas) in 1989 and 1998, respectively. The horizontal shaded regions in yellow indicate the range in captures per 100 mist net hours of effort prior to Hurricane Hugo (1980). Time periods are indicated by red arrows: A, pre-Hurricane Hugo; B, post-Hurricane Hugo; and C, post-Hurricane Georges. Statistical analyses were not conducted for periods with < 5 data points because of a lack of power. Captures declined significantly after Hurricane Hugo (time period B) for all birds ( $B_1 = -0.056$ ,  $P = 0.026$ ) as well as for the Puerto Rican Tody, based on a lenient  $\alpha$  of 0.10 ( $B_1 = -0.123$ ,  $P = 0.059$ ). Analyses used  $\ln$ -transformed capture rates and a quasi-Poisson model.

Figure 10

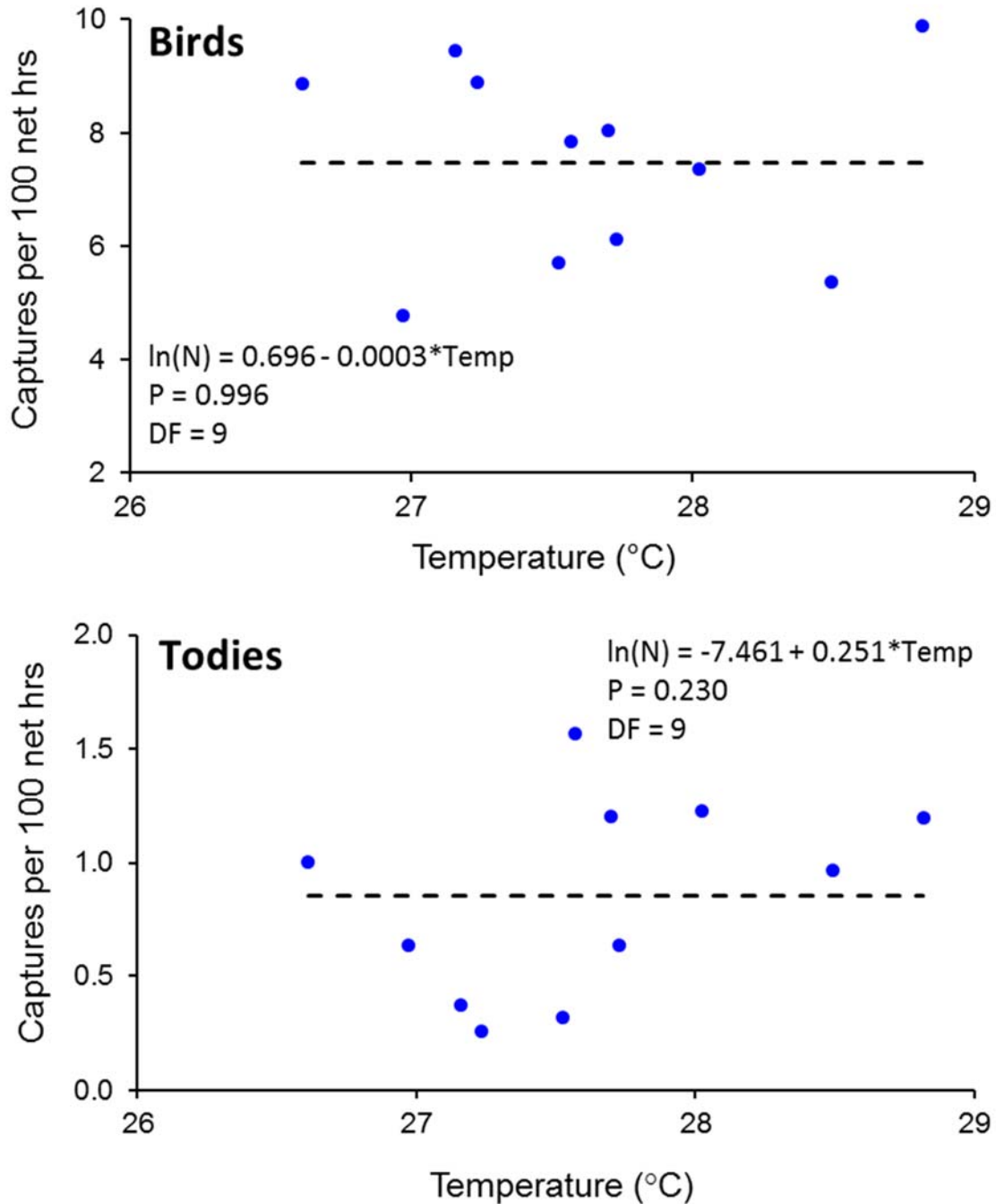


Figure 10. Long-term variation between abundance (captures per 100 net hours) and mean maximum daily temperature for all birds except for the Ruddy Quail-Dove (upper panel) and for the Puerto Rican Tody (lower panel) at El Verde. Analyses were restricted to 1993 to 2005, as these years corresponded to the more recent and compatible climatic records. Abundance did not vary significantly with temperature for all birds ( $B_1 = -0.0003$ ,  $P = 0.996$ ) or for the Puerto Rican Tody ( $B_1 = 0.251$ ,  $P = 0.230$ ). Analyses used In-transformed capture rates and a quasi-Poisson model.

Figure 11

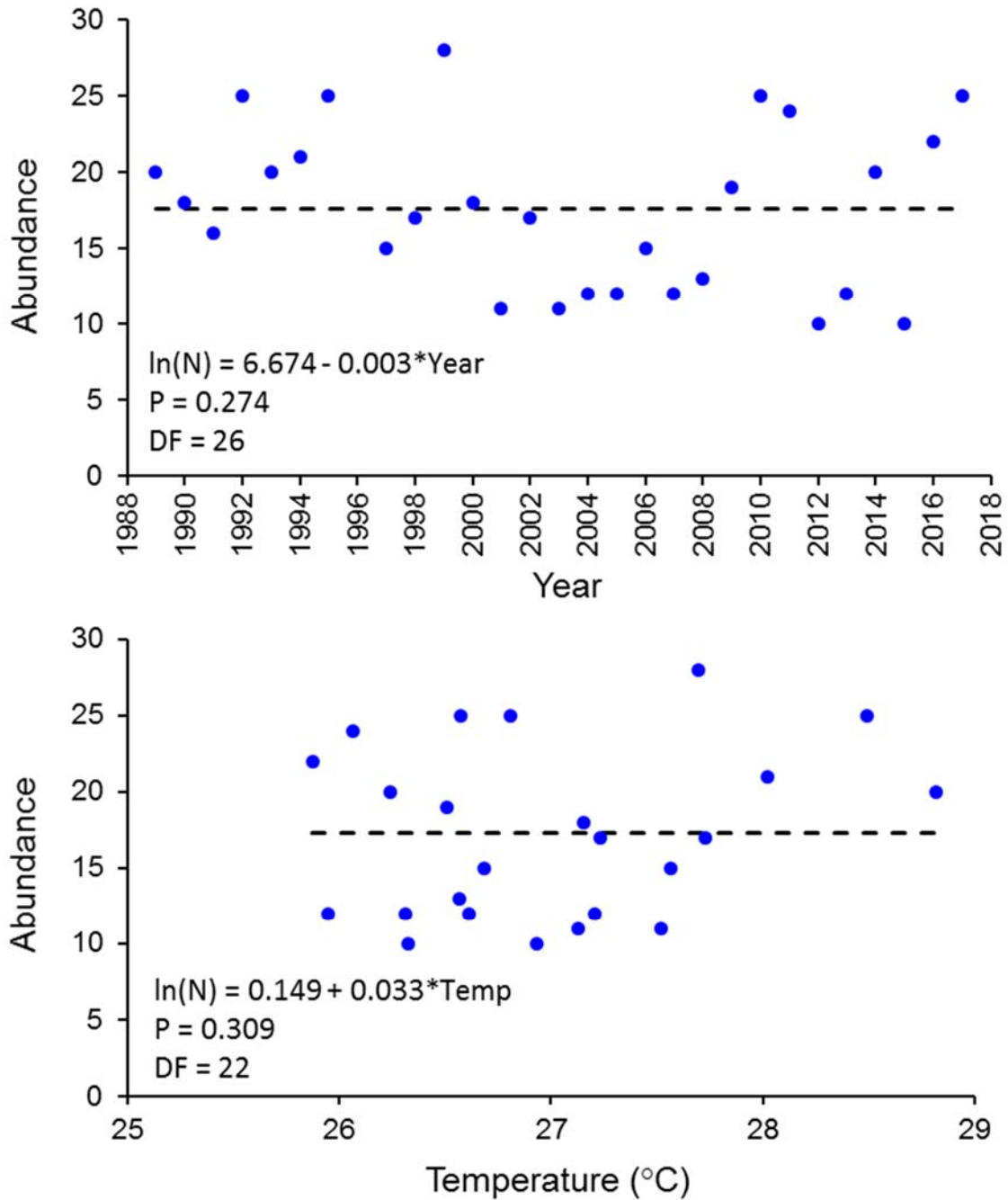


Figure 11. Variation in abundances (total number of individuals at 40 points) of the Puerto Rican Tody on the Luquillo Forest Dynamics Plot with respect to time (upper panel) and temperature (lower panel). Abundance did not vary significantly over years ( $B_1 = -0.003$ ,  $P = 0.274$ ) or with variation in temperature ( $B_1 = 0.033$ ,  $P = 0.309$ ). Analyses used In-transformed counts and a quasi-Poisson model.