5-1-2015

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Recommended Citation

Ryan, Mason J.. "TOO WET FOR FROGS, TOO DRY FOR LIZARDS: ROLE OF CHANGING PRECIPITATION ON TROPICAL FROGS AND ARID LIZARDS." (2015). https://digitalrepository.unm.edu/biol_etds/97

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TOO WET FOR FROGS, TOO DRY FOR LIZARDS: ROLE OF CHANGING PRECIPITATION ON TROPICAL FROGS AND ARID LIZARDS

by

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DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy
Biology

The University of New Mexico
Albuquerque, New Mexico

May 2015

ACKNOWLEDGEMENTS

I have been very fortunate over the course of my career as a field biologist to have numerous people pushing and encouraging me to go back to graduate school…twice. As my field experience and expertise grew, my mentors pushed me towards developing critical thinking and quantitative skills to allow me to be a better researcher. Against my poor judgment and severe imposter syndrome I followed their advice and loving harassment (and at times guilt tripping) to produce this PhD. I will be forever indebted to these people for seeing the potential in me that I did not see. These wonderful mentors are: Dr. Richard Andrus, Dr. Victor Lamoureux, Dr. A. Carl Leopold, Dr. Jay M Savage, Dr. Norman J Scott, Dr. Karen R Lips, Federico Bolaños, Gerardo Chaves, and Jack Ewing.

I am grateful to my PhD advisor Dr. Steve Poe for taking a chance on me and accepting me into his lab. Our shared passion for tropical field work and love of the Simpsons are the real reasons I think he accepted me, but his decision has worked out for both of us. Without Steve's advice, guidance, and unique perspective on ecology I would certainly be a more myopic thinker with regard to ecological problems. Our contrasting research foci, evolution and phylogenetics for Steve, and more ecology-based for me, has greatly helped me become a more well-rounded and productive researcher. The evidence for this can be seen in the eight peer-reviewed papers he and I have published together.

I owe Dr. Joseph Cook a great debt for allowing me to convince him to resurrect the UNM Tropical Biology Course, which was used to generate much of dissertation data. To date we have published two papers from this effort and I'll be able to write many more over the years. Joe has become a good friend and mentor and has been integral in my growth as a person and a scientist.

I am overly thankful that Dr. Howard Snell agreed to be on my committee. Howard has always been fun to talk to about herpetological natural history and helping me put these observations into a critical context. I tend to get overly excited about preliminary data and Howard would always reign me in and keep me honest. His unique insights and expertise in reptile ecology made this frog biologist a more well-rounded herpetologist. Furthermore, he always allowed me access to his wonderful reptile library.

I have been fortunate to make many wonderful friends and colleagues while at UNM. Without their kindness and support I would not be here and would not have been successful.

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ABSTRACT

During the course of the Anthropocene, humans have modified the landscape and atmosphere resulting in increased global temperatures and intensification of the hydrologic cycle over the last 100 years. Amphibians and reptiles are especially vulnerable to climate change because of their ectothermic physiology and sensitivity to changes in water availability. The role of moisture or precipitation in ectotherm responses to climate change has not been well studied, but moisture plays a vital role in all aspects of the lives of lizards and frogs. It is exceedingly difficult to study the ecological effects of changing precipitation patterns due the stochastic nature of rainfall events. Obtaining accurate and local rainfall measurements is problematic, as is having population and community data covering multiple years. During the course of my dissertation I collected five-years of data on two tropical leaf-litter frog communities in

Costa Rica and three-years of data on an arid lizard community data in New Mexico. Because I incorporated accurate and local rainfall and temperature measurements, I was able to address the role of changing rainfall on these disparate herpetofaunal communities. This dissertation focuses on how frogs and lizards respond to changing precipitation patterns and events at multiple spatial and temporal scales. My first chapter deals with how five species of tropical litter frogs that occur in two distinct elevationally separated environments, respond to changing environmental factors over 42-years. Significant changes in dry season rainfall were associated with species and population specific responses between the two elevations. Chapter Two deals with how a mid-elevation frog community responded to the extreme La Niña event of 2010-2012. Extreme rainfall during 2010-2012 resulted in over population declines and a drop in species diversity, but the community returned to pre-La Niña levels within 13-months following a return to normal rainfall conditions. Chapter Three focuses on the effect of short-term rainfall on a lizard species in New Mexico. Contrary to previous work, my work shows that rainfall, not temperature, influences lizard microhabitat use, and that shade may act as a buffer against dry conditions.

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CHAPTER 1

Introduction

There is growing scientific and societal interest in understanding how species will respond to the multifaceted components of climate change. Current estimates suggest that one-fifth of all species are classified as threatened, with climate change being a primary driver of risk vulnerability (Hoffman et al. 2010; Hof et al., 2010). The majority of our current knowledge of species responses to climate change has focused on the increased temperatures (Parmesan 2005; Dillon et al. 2010; Cahill et al. 2012; Seebacher et al. 2014). Increased global temperatures and plant and animal responses to thermal niche shifts have been relatively well investigated and documented. Species responses have included range shifts in latitude or elevation (Yohe and Parmesan 2003), changes in breeding phenology (Gibbs and Breisch 1999), or population declines related to thermal stress (Sinervo et al. 2010). Along with long-term increases in mean annual temperatures (Hansen et al., 2006), there are shifts in global and local precipitation patterns (Marvel and Bonfils 2013), and an increase in frequency and intensity of large-scale climatic disturbances associated with El Nino Southern Oscillation (Cai et al., 2015). Assessing species responses to changing precipitation patterns or extreme climatic events has received much less attention, but may by equally important to species vulnerability to changing climatic conditions (Suttle et al. 2007; Cahill et al. 2012; Williams et al. 2012).

Water is an essential resource in both arid and tropical ecosystems, driving seasonality, primary production, and timing of animal reproduction (Leigh 1999; Brown & Ernest 2002). Perturbations related to rainfall, such as extreme rainfall and drought conditions, can lead to dramatic cascading impacts to local plant and animal communities.

For example, flooding events in arid environments can reorganize seed-eating rodent communities that take years to recover to the pre-disturbance community structure (Thibault & Brown 2008). Conversely, drought conditions associated with large-scale climatic events such as El Nino can also impact animal communities in a cascading manner. On Barro Colorado Island in Panama for example, the 1992 El Nino resulted in famines of frugivore or granivore mammals when tree flowering and fruiting occurred synchronously in response to the drought conditions (Wright et al., 1999). Following this event it took more than two years for the frugivore and granivore populations to recover to pre-La Nina levels. Furthermore, prolonged droughts can drastically alter entire forest ecosystems leading to ecological state shifts (Collins et al. 2014). Recent droughts in the U.S. southwest are resulting in mass die-offs of drought intolerant tree species, making these systems more vulnerable to large-scale fires and speeding up the state shift process (Gaylord et al. 2013). Thus, the impacts of too much or too little water can be expected to alter community structure of animals in both arid and tropical landscapes, but the duration and patterns of species responses to changing precipitation patterns remains relatively unknown. Increase in frequency and intensity of extreme precipitation events should therefore be expected to elicit responses in animal populations, potentially increasing risk of local extirpations in the coming decades.

Amphibians and lizards are ideal organisms for studying community-wide and population specific responses to global change because of their ectothermic thermic physiology and ease of detection (Pough et al., 2004). Ectothermy makes amphibians and lizards especially sensitive to climate change, and shifts in their thermal niches can produce dramatic physiological responses such as an increase in basal metabolic rates

(Colwell et al., 2008; Deutch et al., 2008; Dillon et al., 2010; Sinervo et al. 2010). Under increased temperatures and associated thermal stress terrestrial ectotherms such as frogs and lizards are expected to experience a decrease in daily activity patterns leading to decreased foraging rates and fecundity, and eventual population extirpations (Sinervo et al., 2010; Huey & Tewksbury 2010). One potential solution in lizards is behavioral thermoregulation, and it has been hypothesized that lizards will be able to increase the use of shaded microhabitats as a thermal buffer under future climate warming (Kearney et al. 2009). The behavioral microhabitat use adjustment may offset the large decrease in daily activity predicted by Sinervo et al. (2010) and allow some populations to persist (Kearney 2013; Clusella-Trullas et al. 2011). What is missing in forecasting ectotherm responses to climate change is the role of precipitation, which is also important in regulating amphibian and lizard behavior and physiology.

Both amphibians and lizards, including eggs and adults, must maintain a proper water balance of they suffer decreased functional ability or outright mortality (Gans and Pough 1982; Wells 2007). Long-term, directional changes in rainfall, as well as extreme events can impact both amphibian and lizard populations (Whitfield et al. 2007). Too much water can cause abrupt changes to important habitat features, lead to drowning of eggs and adults, and alter abundance of prey. Conversely, too little water for extended periods of time can result in hydric stress that limits activity, increase the risk of dehydration, and also effect prey abundances. The effects of drought can also alter the abundance and quality of shaded microhabitats such as trees (Williams et a. 2012; Gaylord et al., 2013), which can have cascading impacts on lizards. Both extremes of the hydrological spectrum can result in potentially negative population responses such as unusually variable population fluctuations on the too wet side, and attrition of individuals and population size over months or years on the dry side of the spectrum.

To more thoroughly understand amphibian and lizard responses to climate change it is necessary to add hydrological changes across the landscape to compliment the thermal ecological aspect. Studying the effects of changing precipitation patterns and extreme climatic events is inherently difficult because of their stochastic nature, but are possible using long-term studies and rainfall manipulation experiments. Long-term, directional changes in precipitation can affect communities on a decadal time-scale and requires baseline community data for comparative purposes. To capture the impacts of a large-scale climatic event such as El Nino or La Nina it is necessary to conduct long-term studies that happen to coincide with such an unpredictable, albeit prolonged event. Finally, addressing and identifying how drought and sporadic rainfall events impact animal behaviors most efficiently requires an ecosystem level rainfall manipulation study. Again, due to the stochastic nature of rainfall events, especially in arid environments, manipulation studies allows for more predictable measurements of animal responses to these pulse events.

In the following chapters of my dissertation I set out to address how climate change induced shifts in rainfall impact tropical leaf litter frogs and one lizard species in an arid environment at different temporal and spatial scales. The first two chapters focus on how leaf litter frog communities in Costa Rica respond to long-term changes in seasonal rainfall and to an extreme La Nina event. The first study addresses how the same five frog species, which occur at two different environments, a lowland rainforest and premontane forest, respond to climatic changes over a 42-year period. We used baseline community data from 1969 and data collected from 2009-2012, to determine if these species showed uniform population changes between sampling periods. We found that species exhibited individualistic responses between and within the two environments, which may be related to long-term decrease in rainfall at one site and a concomitant increase in rainfall at the other site. Chapter Two addresses how an extreme El Nino Southern Oscillation climatic event impacts a tropical leaf litter frog community. During 2010-2012 an exceptionally strong La Nina event occurred global and resulted in record high rainfall amounts in Costa Rica. We found that a leaf litter frog community showed a decrease in density and species diversity that corresponded to the onset of the La Nina event, but rapidly recovered to pre-La Nina levels 12 months after the event ended. The final chapter addresses how lizards of an arid environment behaviorally respond to rainfall pulses in a drought experiment. We found that lizard use of shaded microhabitats is determined by short-term rainfall, not temperature, in Piñon-Juniper woodland. These results suggest that the study species may be more vulnerable to drought than increased temperatures, and their ability to persist in this woodland environment will be dependent on the persistence of trees that provide shade.

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CHAPTER 2

Individualistic Population Responses of Five Frog Species in Two Changing Tropical Environments Over Time

Published in: Ryan MJ, MM Fuller, NJ Scott, JA Cook, S Poe, B Willink, G Chaves & F Bolaños. Individualistic population responses of five frog species in two changing tropical environments over time. PLOS ONE 9(5):e98351.

Abstract

Roughly 40% of amphibian species are in decline with habitat loss, disease, and climate change being the most cited threats. Heterogeneity of extrinsic (e.g. climate) and intrinsic (e.g. local adaptations) factors across a species' range should influence population response to climate change and other threats. Here we examine relative detectability changes for five direct-developing leaf litter frogs between 42-year sampling periods at one Lowland Tropical Forest site (51 m.a.s.l.) and one Premontane Wet Forest site (1100 m.a.s.l.) in southwest Costa Rica. We identify individualistic changes in relative detectability among populations between sampling periods at different elevations. Both common and rare species showed site-specific declines, and no species exhibited significant declines at both sites. Detection changes are correlated with changes in temperature, dry season rainfall, and leaf litter depth since1969. Our study species share Least Concern conservation status, life history traits, and close phylogenetic relationship, yet their populations changed individualistically both within and among species. These

results counter current views of the uniformity or predictability of amphibian decline response and suggest additional complexity for conservation decisions.

Introduction

A primary focus of community ecology is to understand how species respond to environmental variation across space and time [1]. This focus has gained urgency as anthropogenic pressures alter species dynamics [2], pushing many species toward extinction [3]. Long-term studies of community ecology can link shifting population patterns to changes in climate and inform conservation efforts for imperiled species and communities [4,5].

Tropical amphibians are at the forefront of the current extinction crisis [4,6]. As a consequence of climate change, habitat loss, disease, and interactions among these factors, 40% of the 7,125 known amphibian species are at high risk of extinction in the near future [6,7]. Disease-induced population crashes caused by the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) have been documented in many amphibian communities [8], but little is known about long-term population trends and non-disease threats in most species [4,7].

Identifying decadal-scale population trends for tropical amphibians has been difficult due to a dearth of historical baseline population data [9,10]. In one case where such data were available, an entire Neotropical leaf litter amphibian fauna was found to have declined over a 35-year period in the Atlantic lowlands of Costa Rica, with declines linked to climate change [11]. Although long-term site-specific studies provide valuable insights into local population responses to environmental change, they cannot assess interpopulation differences in susceptibility across species' ranges [12,13].

Measuring population changes in multiple environments is particularly important because climate change is not occurring uniformly across the landscape [14]. Instead, changes are localized due to variable conditions (e.g., topography, prevailing winds) resulting in a mosaic of novel climatic conditions at small spatial scales [14–16]. Species with broad ranges may include locally adapted populations that exhibit different tolerances to changing environmental conditions and disease [17–19]. Long-term assessments that incorporate population trends across more than one environment are needed to understand range-wide responses of species to change.

Characterizing interpopulation variation in the environmental sensitivity of amphibian species is critical for developing research and conservation priorities in a rapidly changing world [3,12]. Amphibians are especially sensitive to long-term global climate change because warming temperatures and altered hydrologic cycles are expected to increase thermal stress [20], affect disease susceptibility [21], desiccate breeding habitats [22], reduce availability of critical microhabitats [11,23], and alter foraging behavior and efficiency [24,25]. Yet, because climate change is occurring heterogeneously across the landscape [14], it is unclear if all populations of a species are at equal risk [13].

In the Neotropics, frogs of the clade Terrarana dominate leaf litter vertebrate community diversity and abundance [26–28]. Terrarana frogs reproduce by direct development, have no association with aquatic habitats, and depend on standing leaf litter for most aspects of their life, e.g., refugia, foraging, and egg laying sites [28,29]. Because of their strong leaf litter association and independence from aquatic habitats, many Terrarana frog species are expected to be directly or indirectly more vulnerable to climate change than disease [9,11,30]. There is a wide-range of *Bd*-susceptibility within Terrarana with riparian species being more susceptible to *Bd* compared to the terrestrial species studied here [30—32]. Following *Bd*-declines some strictly terrestrial Terrarana species increase in abundance and become dominant components of post-*Bd* assemblages [30]. By studying non-*Bd* vulnerable frog species it is possible to evaluate the effects of environmental change on the remaining species in a post-*Bd* world.

Here we expand the growing field of longitudinal population comparisons [e.g.,11,33,34] by studying five wide–ranging Terrarana leaf litter frog species in two distinct tropical environments. The broad geographic distributions, syntopy, close phylogenetic relationship, and ecological similarities of these species make them ideal for comparative exploration of long–term population changes. We address relative detection changes within and among species, both within and between environments and over time. We used plot presence/absence data as an assay of relative detection probability from 1969 and 2009—2012 from one Lowland Tropical Forest (51 m.a.s.l.) and one Premontane Wet Forest (1100 m.a.s.l.) environment in southwestern Costa Rica.

Methods

Ethics Statement

The study was approved and conducted under animal care protocol 08UNM041 by the Institutional Animal Care and Use Committee at the University of New Mexico. Costa Rica Research Permits were granted through Javier Guevara at Ministerio de

Ambiente y Energia (MINAE) to MJR. This study did not involve any endangered species.

Study Sites and Field Methods

Las Cruces Biological Station (LCBS) protects approximately 227 hectares of Premontane Wet Forest in the Coto Brus Valley (8.785778 N; 82.958889 W Decimal Degrees; 1100 m elevation) on the Pacific versant of the southern Talamanca Mountains, Puntarenas Province, Costa Rica. The 39–year mean annual rainfall is 3442 mm, with a distinct dry season from January—March, and a mean annual temperature of 20.7° C [Table S1; 35]. LCBS has been protected since 1962 and is surrounded by a matrix of smaller fragments and agricultural land [36].

Fundación Neotropica Station is located ~ 2km southwest of Rincón de Osa (Rincón; 8.69602 N, – 83.50139 W, 51 m) on the Osa Peninsula in the southwest Pacific lowlands, Puntarenas Province, Costa Rica within the lowland Tropical Forest Zone. The region was forested until the late 1960s when a logging camp was established, and by the 1980s deforestation was nearly complete [37]. By 1996 the flatlands had been converted to pastureland, but the adjacent foothills and steep slopes remain largely forested, including approximately 300 hectares of primary and older secondary forest [37]. Because our surveys require relatively flat forest (see below), all studied plots were in the foothills of the forested mountain, approximately 200 m from cattle pastures. Plots were on the Fundación Neotropica Station or within 1 km of the station on adjacent private property. The 52–year mean annual rainfall for Rincón region is 4730 mm with a distinct dry season from January—March, and a mean annual temperature of 27.5° C [Table S1; 38].

Participation of the original researcher, Norman J Scott, allowed us to replicate the field data collection and plot set-up techniques used for the 1969 baselines. Each plot was 25-foot square. The original plots were not resampled and each year new plots were sampled to minimize possible impacts from litter removal disturbances during sampling. Plots were placed haphazardly within the forest in flat areas away from trails, tree fall gaps and slopes; we could not completely randomize plot placement within the forest patches. We used Scott's [26] clearing techniques that require removal of all leaf litter to maximize frog observations per plot. After plots were sampled the leaf litter and debris were added back to the plots. During the dry season of March 1969, Scott [26] sampled 10 plots: five at LCBS and five at Rincón; from 2009—2012 we sampled 78 plots, 38 at LCBS and 40 at Rincón in March. We measured leaf litter depth using a ruler at the corners and center of each plot and averaged these measurements for an estimate of leaf litter depth/plot.

Statistical Methods for Relative Detection Probability

We measured changes in detection probability by scoring the proportion of plots occupied, e.g. presence/absence, for each species during a given sampling period (Summarized in Table S1). This is a statistically simplified approach to estimating detection probability, and we refer to this as relative detection probability. We used this approach because of limitations imposed by the original study design that precluded the use of robust algorithm based detection probability approaches such as Program

PRESENCE [38]. Algorithm based methodologies have specific assumptions in model building that include primary and secondary sampling periods per field season [39]. Our study does not meet these assumptions because we lack a secondary sampling period. Instead, we attempted to exactly replicate the original study, which did not have a secondary sampling period [26].

Although we also collected abundance data, we analyzed relative detection probability rather than abundance because four of our five focal species were present in low numbers (see below) and such over-dispersion may cause problems for non-logistic approaches [40]. To assess changes in species presence/absence over time, we regarded 1969 as the initial sample period, and all samples recorded between 2009 and 2012 as secondary measurements of a repeated measures experiment. We compared the 1969 samples to the later period formed by pooling the 2009—2012 samples. We investigated temporal changes in presence/absence at each site separately and jointly (e.g., by including a time x site interaction term).

We converted the raw species counts recorded from each plot to presence/absence data, and analyzed the resulting occupancies by logistic regression. Statistical modeling was hindered by the condition of the data, which was characterized by low initial samples size and sparse occupancy (i.e., many empty samples). In addition, the repeated measures design, and probable spatial autocorrelation of samples collected from the same site [41], raised concerns that residual errors may be spatially and temporally correlated. The aforementioned data issues are problematic for standard logistic methods, which rely on maximum likelihood calculations to estimate model parameters. The Firth logistic method, which uses a penalized likelihood method, was developed to overcome computational challenges presented by small sample sizes, data sparsity, and non-independence [42]. Therefore, all of our logistic modeling was performed using the Firth method.

In evaluating the contribution of Site and Period to presence/absence, we constructed a separate model for each species. We considered an effect to be statistically significant if the probability of a non-zero coefficient (i.e., alpha) was less than 0.05. All statistical modeling was performed in R [43].

The year 2011 was a strong La Niña year, which resulted in significantly higher than normal rainfall in lower Central America [44] and at our study sites (unpublished data). The intent of our study was to focus on average trends and not exceptional events such as the strong La Niña. We included 2011 in preliminary analyses (which bolstered our current conclusions of population decline; see below), but because it differed from the other recent sampling years we excluded it from analyses presented here due to concerns of conflating long-term trends with changes due to anomalous climatic effects [44].

Climate Trends

We used meteorological data from the Loma Linda and LCBS meteorological stations to explore long-term climate patterns at LCBS. The Loma Linda (8.7385 N; –82.922717; 1100 m) station is located 14 km south of LCBS and includes rainfall and temperature data from 1973—2007. The LCBS station has rainfall and temperature data from 2005—2012. Loma Linda and LCBS had comparable weather for the three years of data shared by these stations (2005—2007; Fig. S1 and S2). Combining data for these stations provided a continuous record from 1973—2012.

There are no complete and reliable meteorological records from any weather station in the vicinity of Rincón. To reconstruct the recent historical temperature and rainfall profile we relied on meteorological data from three regional lowland weather stations. Hacienda Barú National Wildlife Refuge (N 9.27152; – 83.88162 W; 24 m) is located 45 km north of Rincón and has documented monthly rainfall from 1981—2011 and temperature from 2001—2011. The Golfito weather station (8.39 N; – 83.11 W; 15 m) of the Instituto Meteorológico Nacional is located approximately 25 km south of Rincón and has kept monthly rainfall records from 1960—1983. We determined that Hacienda Barú and Golfito receive similar rainfall using the same methods as above for the four years of overlap, 1980—1983 (Fig. S3). The third station is in David, Panama (8.4 N, – 82.424167 W; 27 m) 117 km east of Rincón and the closest Pacific lowland station with long-term monthly temperature data from 1973—2000 [16]. We combined the weather data from these three stations to reconstruct general decadal climate change for the Pacific lowlands near Rincón [16].

We used linear regression to explore long-term changes in rainfall and temperature at each site. The binned wet and dry season rainfall and temperature data allowed us to test long-term, seasonal rainfall and temperature trends. We follow McDiarmid and Savage [38] in classifying months with less than 200 mm of precipitation as dry season (i.e., January—March).

Results

Changes in Relative Detection Probability

We were able to calculate relative detection probability changes for all five species from the plot presence/absence proportions for 1969 and 2009—2012 (excluding 2011) (Table 1). The general Firth logistic regression model results show that relative detection probability significantly changed for three species between sampling periods and one species showed a significant time Period X Site interaction (Table 2).

The site-specific Firth logistic regression results show individualistic changes in relative detection among species and sites. One species, *Craugastor stejnegerianus,* showed no change in relative detection at both sites over time, and the other species exhibited unique changes between sites over time (Table 3, Fig. 1). Three of five species showed a negative change in relative detection at the mid-elevation site, LCBS; two of these species, *C. rugosus* and *Diasporus vocator*, can be considered rare in our samples and were not detected in the later sampling period. At Rincón, two species showed a negative change, *C. crassidigitus* and *C. rugosus; C. rugosus* was rare in our samples and was not detected during the later sampling period (Fig. 1).

Climate Variables

We observed a significant increase in annual mean minimum temperature at Rincón of 0.059° C/year (R^2 = 0.558; *P* = 0.0001) and at LCBS of 0.064° C/year (R^2 = 0.420; *P* = 0.0001) since 1973 (Fig. 2). We found dry season precipitation changed divergently for each elevation. At Rincón, dry season precipitation significantly decreased by 8.47 mm/year on average since 1960 (R^2 = 0.324; DF = 55; *P* = 0.0001).

There was no significant change in wet season ($R^2 = 0.044$; DF = 55; $P = 0.129$) or annual precipitation ($R^2 = 0.006$; DF = 55; $P = 0.554$). Conversely, at LCBS dry season precipitation significantly increased by 2.24 mm/year on average since 1973 ($R^2 = 0.148$; DF = 34; $P = 0.018$) with no significant change in wet season ($R^2 = 0.028$; DF = 34; $P = 0.339$) or annual precipitation ($R^2 = 0.042$; DF = 34; $P = 0.242$).

Litter Depth

At LCBS mean leaf litter depth decreased significantly from 7.02 ± 2.11 cm (Std Dev) in 1969 to 4.88 ± 1.69 cm in the 2000s (Kruskal-Wallis $\chi^2 = 4.425$; DF = 1; $P = 0.037$). At Rincón mean leaf litter depth exhibited no significant change between March 1969 and the 2000s (Kruskal-Wallis $\chi^2 = 1.553$; DF = 1; $P = 0.219$).

Discussion

Relative detection probability changes in the five frog species indicate two broad patterns in time and space that are associated with substantial changes in temperature, dry season precipitation and leaf litter depth. First, the site-specific results show relative detectability changes varied among species between sites, with neither site exhibiting uniform declines across all species between 42–year sampling periods (Fig. 1). Second, we observed substantial intraspecific variation in different environments between 42-year sampling periods. Our results suggest that these widely distributed leaf litter frogs show individualistic responses to environmental change, a pattern that fits the individualistic or Gleasonian ecological view [12,45].

The scope, design and results of our study differ from previous tropical amphibian decline studies in three main ways. First, previous amphibian population change studies documented community–wide declines within a single locality and environment (i.e. lowland rainforest or montane cloud forest) [11,46,47]. Our study measured simultaneous changes in the same five species across two distinct environments over time and found no uniform, community-wide decline. Our approach assessed inter- and intraspecific responses at broader geographic scales than previous work. Second, previous mid-elevation amphibian decline studies have focused on highly *Bd*-vulnerable riparian species that quickly declined [i.e., 30,47,48] rather than terrestrial leaf litter species that are likely to be more vulnerable to climate change than *Bd* [9,11,30]. Our focus on non-*Bd*-vulnerable leaf litter frogs, 20-years after *Bd* arrived in the region (e.g. early 1990's) (32), allowed us to investigate responses associated with climate change rather than the confounding or direct effects of disease. Third, we rely on changes in relative detection, instead of the more commonly used count data [11,48], to measure if species have become more rare over time. This approach is more conservative than using count data to assess population change because it is less vulnerable to overestimating the magnitude of change for species with low sample sizes [49].

Amphibian populations are susceptible to stochastic variation and distinguishing natural amphibian population fluctuations from directional short- or long-term declines has been problematic [50,51]. Extreme population fluctuations tend to be driven by unpredictable changes to aquatic breeding habitats, droughts, or deluges, impacting aquatic breeding species more than terrestrial breeding species [51,52]. With no ties to running or standing water for reproduction, Terrarana frogs are not expected to exhibit short-term population fluctuations characteristic of aquatic species [11,52]. Because the sampling years in our analysis represent periods of relatively constant weather (Fig. 2) it is unlikely our patterns reflect short-term changes. During the 2011 sampling year that we removed from analysis, both sites received approximately 50% more rainfall than the long-term means. We excluded this year in order to maintain comparability with the early (1969) sampling period, which received an unexceptional amount of rain.

Site-Specific Patterns

Because our study species are phylogenetically closely related and ecologically uniform, similar population responses to environmental change might be expected [30,53]. Yet we observed individualistic responses among species, with no general community wide trends at either site despite significant changes in temperature and dry season rainfall (Fig. 2). This result is consistent with patterns observed in North American small mammals and birds. Moritz et al [33] found elevational range shifts to be variable among small mammal congeners over a 100-year period [33]. Taper et al. [12] found differing patterns of decline among species of insectivorous songbirds. These examples of species-specific responses highlight the complexity of predicting individual species and community responses to climate change.

Why did we observe species-specific responses among closely related, ecologically similar frog species? We can only speculate on mechanisms. Body size is an important predictor of species extinction threat from disease or climate change with large species at greater risk than small species [32,54], but there is no relationship of body size and population trends among our species (Fig. 2, Table 1). We hypothesize that undetected micro–ecological differences (breeding phenology, diet, etc.) will emerge with future study of these species. For example, *Diasporus vocator* may have declined at LCBS because increased dry season rainfall saturated the soil leading to high rates of egg mortality [55]. Increased dry season rainfall was not evident at Rincón, and perhaps the eggs of *D. vocator* are especially sensitive to changes in rainfall patterns. This scenario is speculative, as we do not understand the ecology of *D. vocator* at this fine level. Autecological studies of our five frog species are needed to shed light on their varying responses.

Intraspecific Patterns

Observed differences in relative detection changes within species show that these leaf litter frogs respond to long-term environmental change individualistically. The majority of our species showed a decrease in detection at one site but not the other site between the 42-year sampling periods (Fig. 2). A similar result has been found in birds, where 77% of 47 species that occurred in more than one environment varied in degree of population change between environments [12].

These individualistic responses could be attributed to varying environmental stressors at each site differentially affecting traits that are constant across species (see previous section). Alternatively, local variation in decline susceptibility within species may produce our observed patterns. For example, *Craugastor crassidigitus* declined at Rincón but not LCBS. Temperature increased significantly at both sites, so perhaps the population of *C. crassidigitus* at Rincón is sensitive to warmer temperatures but the population of *C. crassidigitus* at LCBS is tolerant to increased temperatures. Such a scenario likely oversimplifies the complexities of ecological interactions that may be operating. Additional factors such as invertebrate predation [56] and physiological stresses associated with increased temperatures and altered rainfall patterns [20,57], or other dynamic interactions, may drive local changes. Regardless of the mechanisms, intraspecific variation in response to local environmental change is evident among both common and rare species.

One species, *Craugastor rugosus,* was rare at both sites in 1969 and not detected during the later sampling period (Table 1) and warrants special consideration. Because we did not detect *C. rugosus* during the later sampling period, we would infer that this species was locally extirpated. However, we conducted transect surveys to supplement the plot method and detected *C. rugosus.* Detection of this species using a secondary method contradicts the inference from our plot data. We suggest that when replicating historical population comparisons to assess declines, alternative survey methods should be employed to detect rare species. Such multifaceted approaches are especially needed when assessing population extirpations. Reliance on a single field survey method may overestimate a species' threatened status.

Finally, due to the ubiquity of *Bd* in Costa Rica and it's role in amphibian declines we cannot rule out the possibility that at least some of our observed changes are related to disease. This is more of a concern at LCBS than Rincón because no severe *Bd*-declines and die-offs have been reported at tropical lowland sites, despite *Bd* being detected at low elevations [58,59]. *Bd* arrived in the LCBS region in 1993, almost 20-years before our later sampling period [32]. There is no rigorous documentation of the *Bd* die-off at LCBS, but many Bd-susceptible species such as *Atelopus varius*, *Craugastor ranoides*, and others are now absent from the frog fauna [60]. It is not possible for us to determine whether *Bd* played a role in the decline of our study species at LCBS. However, we note that Picco and Collins [61] detected *Bd* at LCBS but did not detect *Bd* on any strictly terrestrial, direct-developing frog species there, including two of our study species. Furthermore, our study species and their relatives are known to increase in community dominance [30] and abundance [62] within four years of *Bd*-related faunal collapse. We suspect that *Bd* has had an impact on many amphibian species at LCBS. However there is no evidence that any of our study species has been affected.

Conclusions

We documented individualistic changes of frog populations between a 42—year period at two distinct sites. Observed changes are associated with increased temperatures, altered dry season rainfall, and changed leaf litter depth, all of which influence leaf litter amphibian populations [7,11].

Increased rarity in some populations and not others is both troubling and optimistic in terms of long-term persistence of these leaf litter frogs. Our results are optimistic because we did not observe local extirpations of rare or common species despite decades of environmental change and disease emergence. Instead, common species have remained relatively common and rare species have remained rare, albeit at much lower detectability than in the past. This result is not consistent with other Neotropical studies that found declines and extirpations in both common and rare species [11,46,48]. On the other hand, these results are troubling because we detected declines in species of Least Concern not previously reported to have declined [6]. All of our study species have been categorized as Least Concern by the International Union for Conservation of Nature [6]. Population declines in species of Least Concern may be subtler than those of endangered species [63]. The apparently slow population attrition we detected contrasts with the rapid population crashes characteristic of many endangered forms [48,64].

The above concerns clearly are pertinent to conservation decisions, but policy implications are not straightforward. Perhaps instead of focusing on a species as a whole, conservation actions should address local, geographically threatened or declining populations. The complicating factors we have identified, including decline of some populations of Least Concern species, interspecific variation among ostensibly ecologically uniform species, and differing intraspecific responses across space and time, should provide ample material for future discussions of conservation.

Acknowledgments

Thanks to the Organization of Tropical Studies Las Cruces Biological Station and Fundación Neotropica Research Station for allowing access to study sites. We thank Z. Zahawi from Las Cruces and L. Umaña from Fundación Neotropica for permission and logistical support. Permits for research in Costa Rica were granted from MINAE and J. Guevara. We thank Instituto Metereológico Nacional de Costa Rica. We thank the dozens of students in the UNM Tropical Biology Course for assistance in field data collection. This manuscript was greatly improved by suggestions by M. Workman, M. Balk, I. Latella, and three anonymous reviewers. Photograph of *C. stejnegerianus* was provided by K. Christenson.

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Figures and Tables

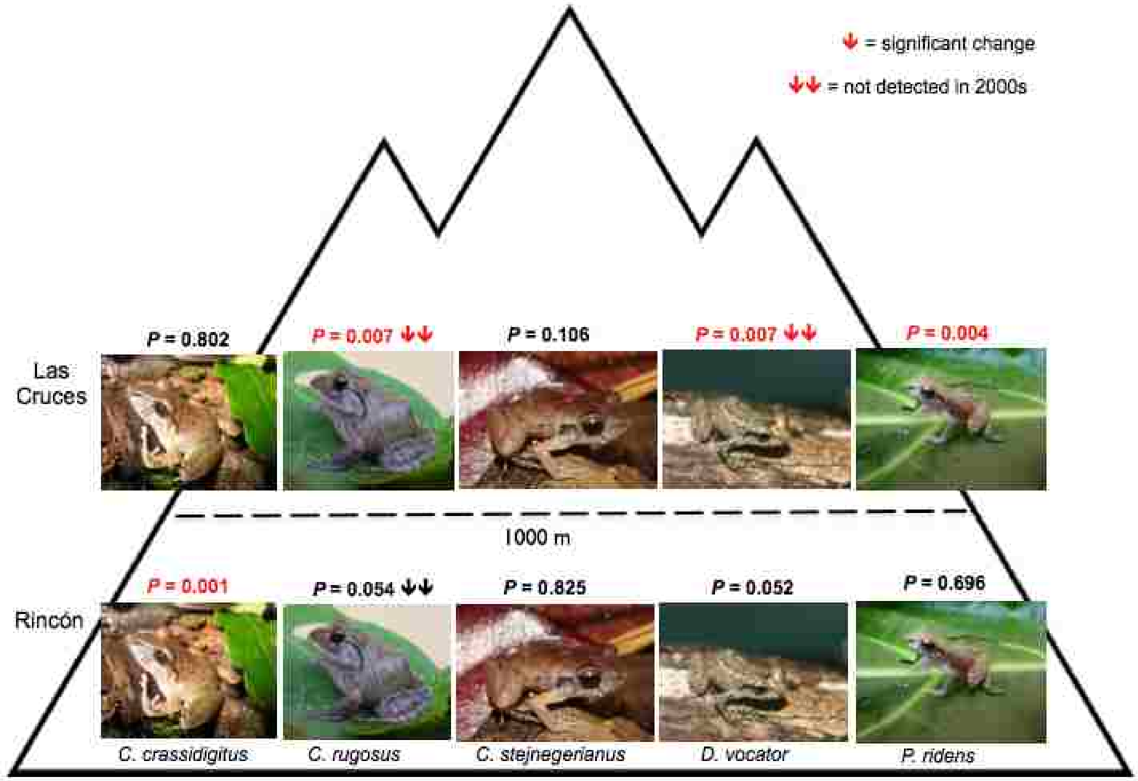

Figure 1. Changes in detection of the five species between the two sites. The site-specific Firth logistic regression *P*–values and direction of relative detection changes between sampling periods and elevation for each species. Upper row is LCBS and lower row is Rincón. See text for details of analysis and Table 1 for raw data.

A.

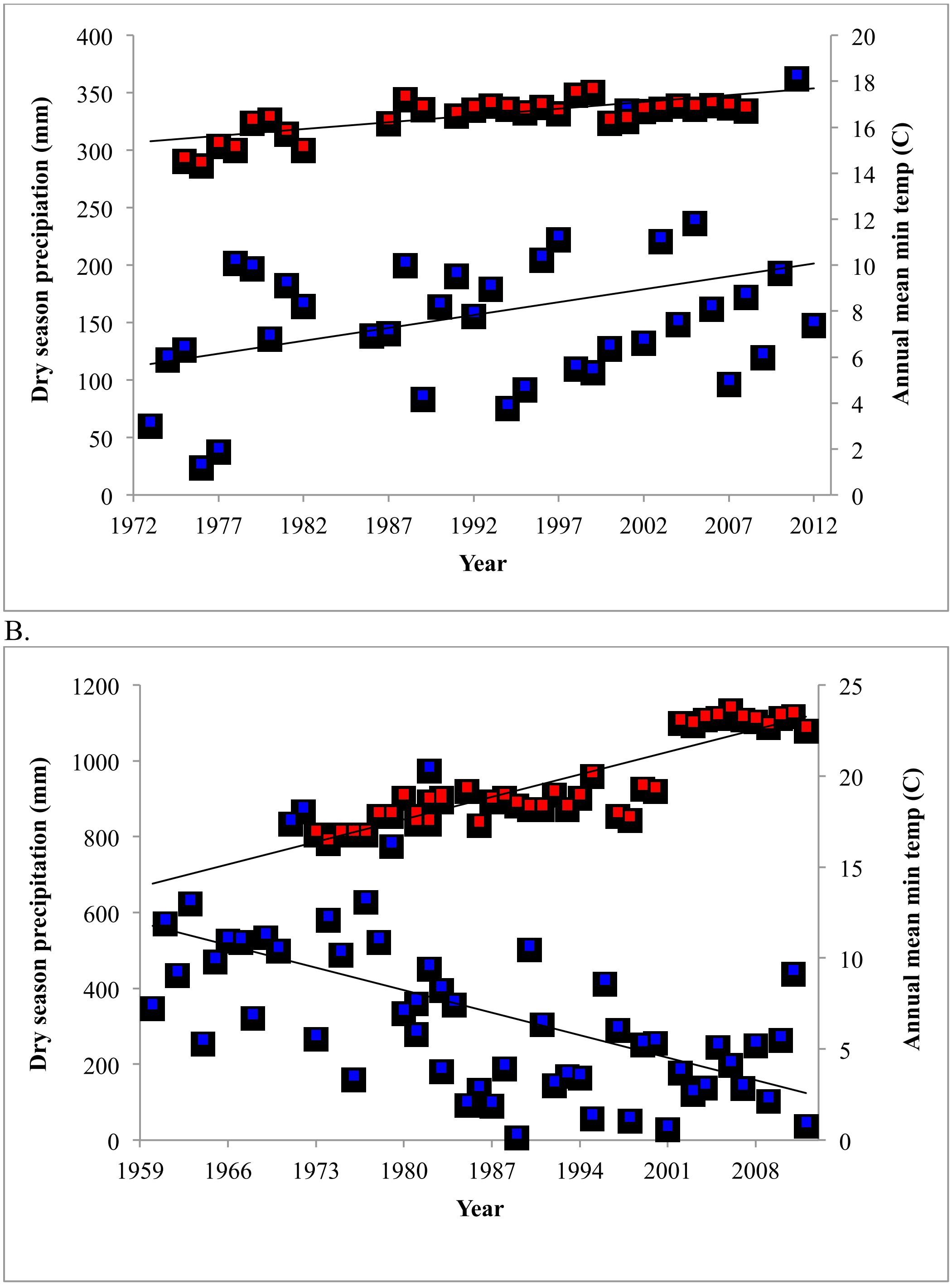

Figure 2. Climatic changes for LCBS and Rincón. Long-term trends in dry season precipitation and minimum annual temperature for A) LCBS and B) Rincón. Red squares represent temperature; blue squares represent dry season rainfall.

Table 1. Plot presence/absence for 1969 and 2000s sampling periods.

Species	LCBS 1969	LCBS 2000s	Rincón 1969	Rincón 2000s
Craugastor crassidigitus	2/5 [20%]	9/28 [32%]	4/5 [80%]	1/30 [3%]
Craugastor rugosus	2/5 [20%]	0/28 [0%]	1/5 [20%]	0/30 [0%]
Craugastor stejnegerianus	5/5 [100%]	17/28 [60%]	5/5 [100%]	27/30 [90%]
Diasporus vocator	3/5 [60%]	0/28 [0%]	2/5 [40%]	2/30 [6%]
Pristimantis ridens	4/5 [80%]	4/28 [14%]	1/5 [20%]	5/30 [16%]

Proportions of plots occupied by each species at LCBS and Rincón between sampling periods. Values in brackets are proportion of plots occupied during that sampling period. These data were used to calculate relative detection probabilities used in the logistic regression analysis. See Table S1 for presence/absence for each individual year.

Table 2. General logistic regression results.

Species	Time Period *P*-value	Coefficient ± STD Error	Site *P*-value	Coefficient ± STD Error	Time Period X Site *P*-value	Coefficient ± STD Error
Craugastor crassidigitus	0.082	-0.23 ± 0.91	0.236	1.44 ± 1.37	0.032*	-2.93 ± 1.54
Craugastor rugosus	0.007**	-3.71 ± 1.71	0.548	-0.76 ± 1.37	0.770	0.69 ± 2.47
Craugastor stejnegerianus	0.106	-1.98 ± 1.66	1.00	0.00 ± 2.29	0.468	1.64 ± 2.39
Diasporus vocator	0.007**	-3.71 ± 1.71	1.00	0.00 ± 1.28	0.385	1.60 ± 2.05
Pristimantis ridens	0.004**	-2.79 ± 1.16	0.076	-2.20 ± 1.46	0.099	2.36 ± 1.62

Logistic regression results relative detection probability calculated from the plot occupancy

See text for details on analyses. Significance levels: * = 0.05; **=0.01.

Table 3. Firth logistic regression results.

Species	Rincón *P*-value	Coefficient ± STD Error	LCBS *P*-value	Coefficient ± STD Error
Craugastor crassidigitus	0.001**	-3.16 ± 1.18	0.802	-0.23 ± 0.99
Craugastor rugosus	0.054	-3.01 ± 1.78	0.007**	-3.71 ± 1.71
Craugastor stejnegerianus	0.825	-0.34 ± 1.72	0.106	-1.98 ± 166
Diasporus vocator	0.052	-2.10 ± 1.13	0.007**	-3.71 ± 1.71
Pristimantis ridens	0.696	-0.44 ± 1.14	0.004**	-2.79 ± 1.16

Site-specific results of Firth logistic regression between sampling periods. ** denotes 0.01 significance level.

CHAPTER 3

Too wet for frogs: changes in a tropical leaf litter community coincide with La Niña

Published in: Ryan MJ, NJ Scott, JA Cook, B Willink, G Chaves, F Bolaños, A García-Rodríguez, IM Latella & SE Koerner. Too wet for frogs: changes in a tropical leaf litter frog community coincide with La Niña. Ecosphere, 6(1):4

Abstract

Extreme climatic events such as the El Niño Southern Oscillation profoundly affect many plants and animals, including amphibians, which are strongly negatively affected by drought conditions. How amphibians respond to exceptionally high precipitation as observed in La Niña events, however, remains unclear. We document the correlation between the exceedingly wet 2010-2012 La Niña and community-level changes in a leaf litter frog assemblage in Costa Rica. Relative abundances of species shifted, diversity and plot occupancy decreased, and community composition became homogenized with the onset of La Niña. These aspects remained altered for over 20-months but rebounded to pre-La Niña levels after approximately 12-months. We hypothesize that complex ecological cascades associated with excess moisture caused short-term declines in abundances of species and associated changes in community structure. If additional stressors such as disease or habitat loss are not co-occurring, frog communities can rapidly recover to pre-disturbance levels following severe climatic events.

Introduction

Environmental perturbations influence species diversity, community composition, and abundances (e.g. Rosenzweig 1995, Thibault and Brown 2008). El Niño Southern Oscillation (ENSO), with two quasi-cyclic phases, La Niña and El Niño, is the greatest source of rainfall variability in the tropics and disrupts terrestrial ecosystems (Holmgren et al. 2001). La Niña may bring extraordinarily high levels of precipitation to the humid tropical regions of southern Central America, northern and eastern Amazonia, and the Pacific Rim, whereas El Niño triggers drought conditions to these same regions (Trenberth 1997, Malhi and Wright 2004). Both phases can profoundly affect terrestrial ecosystems. When El Niño creates drought conditions there is increased tree mortality (Condit et al. 1995) and changes in forest community structure (Enquist and Enquist 2011). Such large-scale effects reverberate through animal populations and communities (Gibbs and Grant 1987, Wright et al. 1999). La Niña events on the other hand, should be expected to impact animal populations from increased soil moisture content and subsequent higher net primary productivity (NPP; Bastos et al. 2013), but the cascading effects of La Niña in regulating animal populations remain relatively unknown. With ENSO events expected to increase in frequency and intensity in the coming decades (Power et al. 2013), understanding how animal populations respond to both phases of ENSO cycles will be imperative if conservation efforts in the tropics are to be successful.

Terrestrial leaf litter amphibians are important predators in the leaf litter environment and play a crucial role in nutrient cycling, energy flow, and carbon storage of forest ecosystems (Davic and Welsh 2004, Best and Welsh 2014). Their importance stems from high population densities and efficiency at converting invertebrate biomass to vertebrate biomass (Best and Welsh 2014). Moisture is a key factor regulating leaf litter predator-prey dynamics (Walton 2013), and variable rainfall has been shown to alter the invertebrate prey base of leaf litter amphibians (Levings and Windsor 1984). Most of the work on leaf litter amphibian ecology comes from temperate forests (Davic and Welsh 2004), but tropical species also are expected to be ecologically important and sensitive to rainfall variability (Best and Welsh 2014, Ryan et al. 2014).

Many amphibians respond negatively to dry periods due to strong dependence on moisture for breeding and water balance (Taigen et al. 1984, Mac Nally et al. 2014). For example, Stewart (1995) reported a major decline in *Eleutherodactylus coqui* with drought, but for 5-years prior to and 3-years following that event adult frog densities showed little annual variation. The effects of too much water on leaf litter amphibians, however, are not well understood. Aquatic breeding amphibians may be more vulnerable to altered rainfall patterns than tropical direct-developing leaf litter species because of the major effects of drying and flooding of ponds and streams compared to the relative stability of the leaf litter habitat (Marsh 2001, Green 2003). For example, the direct developing frog *Craugastor punctariolus* showed no annual population fluctuations and had high survivorship over a 4-year period in Panama, prior to a disease related population crash (Ryan et al. 2008). Thus, the drastic annual population fluctuations that have been associated with altered rainfall patterns observed in aquatic breeding amphibians are not expected for terrestrial amphibians (Green 2003, Walls et al. 2013, Mac Nally et al. 2014).

Tropical amphibian community responses to La Niña have not yet been critically evaluated, presumably because few studies have occurred before, during, and after such an event (but see examples in mammals; Wright et al. 1999, Thibault and Brown 2008). The 2010-2012 La Niña event was the most extreme in 80 years resulting in widespread biotic and abiotic disturbances including increased global rainfall, soil water content, and NPP (Boening et al. 2012, Bastos et al. 2013). The emergence of the 2010-2011 La Niña provided a serendipitous natural experiment to assess how an extreme climatic event affects species diversity and community composition of tropical leaf litter frogs. We measured annual species diversity and community composition of a premontane leaf litter frog assemblage at Las Cruces Biological Station (LCBS) in southern Costa Rica pre-, during, and post-La Niña. Despite previous studies finding terrestrial tropical frog populations to be relatively stable (e.g. Marsh 2001, Green 2003), we predicted changes in community structure and relative abundance due to the severity of this La Niña event, and a slow recovery to pre La-Niña structure.

Methods

Study site & data collection. LCBS protects ~300 hectares of Premontane Wet Forest in the Coto Brus Valley (Decimal Degrees: N 8.785778; W – 82.958889; 1100 m elevation) on the Pacific versant of the southern Talamanca Mountains, Puntarenas Province, Costa Rica. Protected since 1973, LCBS consists of primary forest, old secondary forest, and edge habitats. The 37-yr mean annual rainfall is 3442 mm, with a distinct dry season from January-March and a 29-yr mean annual temperature of 20.57° C (Ryan et al. 2014). The leaf litter frog community at LCBS consists of four direct-developing species – *Craugastor crassidigitus*, *C. stejnegerianus*, *Pristimantis cruentus*, and *P. ridens* – that rely on the leaf litter habitat for egg laying, feeding, and daily refuge for all or most of their lives (Scott 1976, Ryan et al. 2014).

Sampling occurred once per year during March (dry season) in old secondary/primary forest at LCBS. We replicated Scott's (1976) plot survey technique of total leaf litter removal within each plot to maximize frog captures. We sampled 10 plots/year (8 plots for 2012), and half of the species were represented by <10 individuals/year. We calculated species diversity indices for each plot during each sampling year. Plots were 7.6 X 7.6 m (58 m^2) and a 1 m path was cleared around each plot boundary. Plots of this size have proven effective for sampling tropical leaf litter frogs, especially our target species (Scott 1976, Jaeger and Inger 1994). Species identity and number were recorded for each plot. We coded species plot occupancy for each species as 1 when present and 0 when absent. After sampling, litter and debris were distributed back into plots. We used LCBS rainfall measurements to explore annual and seasonal rainfall variability from 2008-2013. Because frog sampling occurred in March, we summed monthly rainfall for the preceding 12 months (i.e. March to February, beginning in 2008-2009).

Statistical analyses. To assess changes in species diversity, we used the sample-based non-parametric Chao1, Chao2, and incidence-based coverage estimator (ICE) diversity indices calculated in EstimateS software v 9.1 (Gotelli and Colwell 2011, Colwell 2013). We selected these species richness estimators because they are most appropriate with small sample sizes and they incorporate species abundances (Gotelli and Colwell 2011).

We used a modified Before-After Design with Kruskal-Wallis test (Smith 2002) to determine the magnitude of change in diversity metrics. For plot occupancy, we used the same approach with an ANOVA, which is suitable for observations associated with natural events. Data collected prior to an event are compared to data during and after the event (Smith 2002). We used this approach because the 2010-2012 La Niña effects were geographically widespread, and therefore, a control treatment was not possible. Using pre-La Niña as the control, we examined the change in species diversity, community composition, and community heterogeneity between pre-La Niña to La Niña and pre-La Niña to post-La Niña. We grouped sampling years into pre-La Niña, La Niña, and post-La Niña categories (Hu et al. 2014). We categorized 2009-2010 as pre-La Niña because the La Niña conditions began after the March 2010 sampling; 2011-2012 was categorized as La Niña; and 2013 was categorized as post-La Niña because conditions were ENSO neutral for the preceding 10 months (Hu et al. 2014).

To examine changes in the relative abundances of each species, we plotted the proportion of total captures and density (frogs/100 m^2) during a sampling period of a single species through time. Differences in the mean and the dispersion of the terrestrial frog community associated with La Niña stage were tested using PERMANOVA and PERMDISP (PERMANOVA v.6). A dummy variable of 1 was added to every plot to account for the high numbers of zeros in plots.

Results

Twelve-month (i.e. March to February) rainfall was greatest during the 2010-2011 period, the peak of the La Niña, with the other years closer to the 37-year mean (Fig. 1a;

note relatively constant temperatures). Between 2009-2010 and 2010-2011, rainfall increased from 3141 mm to 4980 mm (43% greater than the 37-year mean). For the 2010-2011 period, wet and dry season rainfall was 45% and 131% greater than the 37-year seasonal mean, respectively (Fig. 1b). La Niña conditions persisted in 2011-2012, but were considerably weaker (e.g. Hu et al. 2014). Annual and seasonal rainfall levels during this period were similar to non-La Niña periods (Fig. 1a&b).

Frog community structure was similar for 2009 and 2010, but became restructured during the La Niña, as species were lost (Fig. 2a). This leaf litter frog community was composed of four species; all were detected in the first year of sampling (2009). Pre-La Niña, the community was dominated by two species of *Craugastor*; however, during La Niña the second most dominant species decreased drastically only to recover to the dominant position post-La Niña (Fig 2a). Species reordering occurred throughout the La Niña cycle. Species richness also decreased to two during the La Niña but returned to four species post-La Niña. The Chao1, Chao2 (Fig. 2b), and ICE (Fig. 2c) diversity measures were stable during pre-La Niña years, decreased sharply during La Niña years, and returned to pre-La Niña levels in the post-La Niña year. The abrupt changes in species diversity metrics between pre-La Niña to La Niña and La Niña to post-La Niña were all significant, except for Chao1 between pre-La Niña and post-La Niña (Table 1).

Pre-La Niña mean frog community was statistically different from the La Niña mean frog community (Fig 2d; PERMANOVA: t=2.6952, p=0.003); however, mean frog community was not statistically different between pre and post-La Niña (Fig. 2e; PERMANOVA: t=1.2455, p=0.208). Dispersion of plots in community space also decreased significantly from pre-La Niña to La Niña (Fig. 2d; PERMDISP: t=4.019, p=0.003), while pre- and post-La Niña communities had similar levels of dispersion (Fig. 2e; PERMDISP: t=0.732, p=0.509).

We found significant changes in plots occupied during this La Niña cycle (Fig. 3). More plots were occupied during the pre-La Niña period than during the La Niña for all species combined (F-Ratio = $8.66_{1,38}$; P = 0.005). Post-La Niña plot occupancy rebounded to pre-La Niña levels (F-Ratio $1.91_{1,28}$; P = 0.177). Plot occupancy for all individual species decreased during La Niña, but species showed individualistic recovery responses (Fig. 3). Annual density of each species was relatively stable for the two pre-La Niña years, and all show a decline in density in either the first or second year of the La Niña event (Fig. 4). Densities post-La Niña show individualistic increases, but remain below pre-La Niña levels.

Discussion

The 2010-2012 La Niña provided an unusual opportunity to measure the response of a tropical amphibian community to extreme rainfall. Correlation of abrupt changes in species diversity and plot occupancy with the onset of the La Niña is consistent with our prediction that La Niña would have an impact on this leaf litter frog community. Terrestrial frog populations apparently can be influenced by extreme rainfall events similar to aquatic species (Marsh 2001, Green 2003). Although naïvely it might be expected that increased rainfall would not negatively affect terrestrial, leaf litter frogs because of their dependence on mesic conditions, we found that all four species decreased in abundance coinciding with increased annual and seasonal rainfall. Multiple measures revealed strong changes in community structure with marked decreases in diversity and plot occupancy and changes in species rank during this La Niña climatic disturbance, but these measures rebounded by 2013 with the return to normal precipitation levels.

Community responses suggest that these leaf litter frogs are sensitive to extreme periods of rainfall but are resilient and recover once conditions return to normal. Community composition (both species identities and abundances) shifted during the wet La Niña years as species reordering occurred and as species were lost from the community. In addition, plots became more similar, creating a more homogenous frog community compared to the pre-La Niña frog community. The post-La Niña frog community appears to have recovered with species gain occurring and an increase back to pre-La Niña heterogeneity among plots. Both responses are consistent with the idea that although the La Niña strongly impacts frog community composition and heterogeneity, frog communities can recover quickly. The species diversity changes and population fluctuations we observed are not typical of direct developing tropical species (Green 2003), but instead are similar to fluctuations observed following catastrophic hurricanes in Puerto Rico (Stewart 1995).

These abrupt community changes may be driven by short-term changes in the leaf litter environment (e.g. Donnelly and Crump 1998, Lensing and Wise 2007). We propose two hypotheses for mechanisms driving changes in this assemblage during heavy La Niña rainfall such as 2011. Both of these hypotheses depend on direct and indirect effects of excess moisture on the forest floor. First, increased mortality of eggs may result from greater moisture in the leaf litter environment. Terrestrial amphibian eggs require moist conditions to avoid desiccation, but too much water can also be problematic due to disruption of oxygen diffusion leading to death or stunted development (Taigen et al. 1984, Seymour 1999). The extreme rainfall in 2010-2011 in both the wet and dry season likely resulted in temporarily saturated soil conditions at LCBS similar to those observed in other tropical regions during this time period (Boening et al. 2012, Bastos et al. 2013). Above average wet season rainfall, especially in October and November would expose frog eggs to a saturated environment when many leaf litter frogs oviposit (Watling and Donnelly 2002).

Second, excessive rainfall has the potential to alter resource availability in the leaf litter and negatively affect frogs through complex interactions in altered prey dynamics (Lensing and Wise 2007). Observational and experimental studies have identified a positive relationship between litter depth, arthropod abundance (Sayer et al. 2010, Oxford et al. 2013), and litter frog diversity and abundance (e.g. Watling and Donnelly 2002). In general litter invertebrate abundances are higher in the dry season (Levings and Windsor 1984), and the above-average dry season rainfall of 2011 may have disrupted leaf litter dynamics and negatively impacted leaf litter invertebrates. Increased moisture increases leaf litter decomposition rates and abundance of litter shredding invertebrates, resulting in decreased habitat quality and abundance of preferred prey of litter predators (Sayer et al. 2010, Walton 2013). The increase in litter shredding invertebrates may not off-set decreases in preferred prey because they have small body size (Levings and Windsor 1984) and are not commonly found in leaf litter frog stomachs (Toft 1981). Changing leaf litter moisture may indirectly alter litter prey base abundance (Levings and Windsor 1984), creating a mismatch in prey availability and/or hatching timing (Watling and Donnelly 2002, Whitfield and Donnelly 2006, Both et al. 2006). These factors may contribute to population attrition if high moisture conditions persist for an extended period of time such as the 2010-2012 La Niña.

Regardless of the specific factor or combination of factors, leaf litter frogs at LCBS responded to increased rainfall of the 2010-2012 La Niña in a manner not previously observed in terrestrial tropical frogs. We know of no direct comparison of terrestrial animal responses during a wet La Niña event, but in southern South America and the Galapagos, El Niño brings excessive rainfall to arid regions (Malhi and Wright 2004) that are analogous to the La Niña conditions at LCBS of 2010-2012. In Peru, Catenazzi and Donnelly (2007) reported that bottom-up productivity due to increased rainfall restructured a community of gecko lizards. In the Galapagos, Darwin's Ground Finch populations increased with an increase in seed and arthropod resources during El Niño events with high rainfall, with the most extreme El Niño eliciting the greatest response (Grant et al. 2000). These two examples indicate that excess rainfall and resource availability can cause strong ecological responses in arid environments where water is a limiting resource. Observed changes in our study at LCBS suggest that too much water can elicit a strong ecological effect even in environments considered to be moisture-rich.

Many studies have addressed effects of drought on amphibian populations, but few have directly investigated the role of extreme rainfall events (e.g. Bickford 2005, Walls et al. 2013, Mac Nally et al. 2014). This first assessment of La Niña driven rainfall on a leaf litter fauna challenges the assumption that increased water will either benefit or fail to impact terrestrial amphibians. It is unclear how generalizable these results are considering the severity of the 2010-2012 La Niña; nonetheless, leaf litter frogs are vulnerable to stochastic rainfall events. Because extreme climatic events are expected to increase in frequency, ENSO events in the coming century may drive previously sporadic population changes to a new norm (Gibbs and Grant 1987, Power et al. 2013), especially in tropical litter organisms (Green 2003). We suggest that during extreme climatic events amphibian species and communities will be more susceptible to irreversible changes if such events coincide with disease outbreaks, habitat alteration, or other stressors. But, if additional stressors are not a major factor during an extreme event, species diversity and abundance may rapidly recover to pre-climatic disturbance levels.

Acknowledgements

We thank Z. Zahawi and W. Lopez of the Organization of Tropical Studies Las Cruces Biological Station for allowing access to the station and climate data, and three sets of Tropical Biology students from the University of New Mexico and the University of Costa Rica for their field efforts. Permits for research in Costa Rica were granted from MINAE. We thank J.H. Brown, L. A. Fitzgerald, and J. L. Voyles and two anonymous reviewers for comments on the manuscript. A UNM Grove Scholarship, LAII PhD Fellowship, IdeaWild, to MJ Ryan, NSF grant DEB 0844624 to S. Poe, and the UNM Biology Department for helping to fund this project.

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Figures and Table

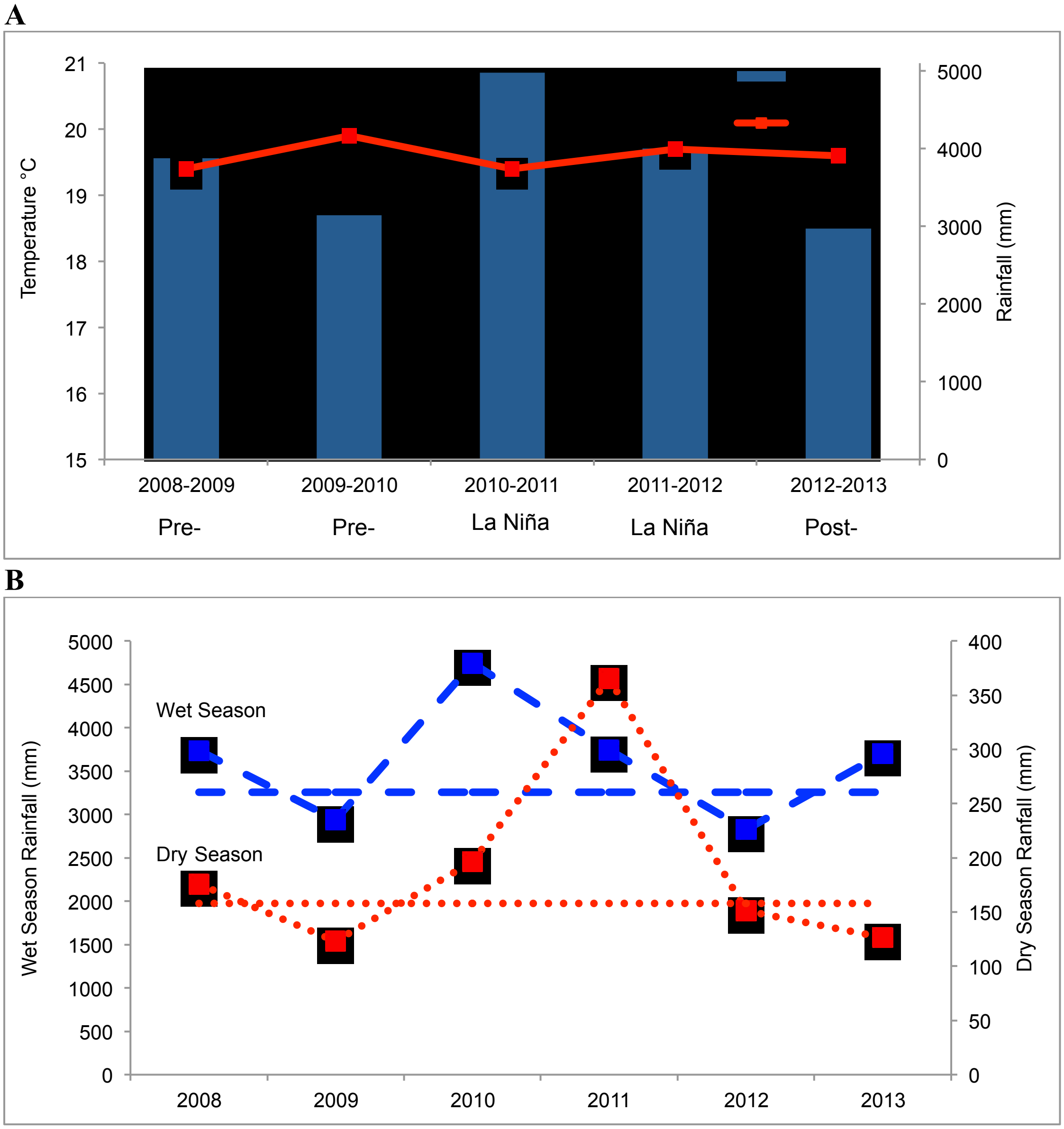

Figure 1. (a) Mean annual temperatures and 12-month rainfall totals measured from March to February for each sampling year. This La Niña was strong from July 2010 to April 2011, followed by a 4-month lull, reemerging to slightly weaker La Niña conditions from September 2011 to March 2012 (Hu et al. 2014). (b) Seasonal rainfall totals from 2008 to 2013. This La Niña was most severe in wet season of 2010 and dry season of 2011. Straight lines represent the 37-year seasonal rainfall mean, and highlight the above average rainfall during the La Niña.

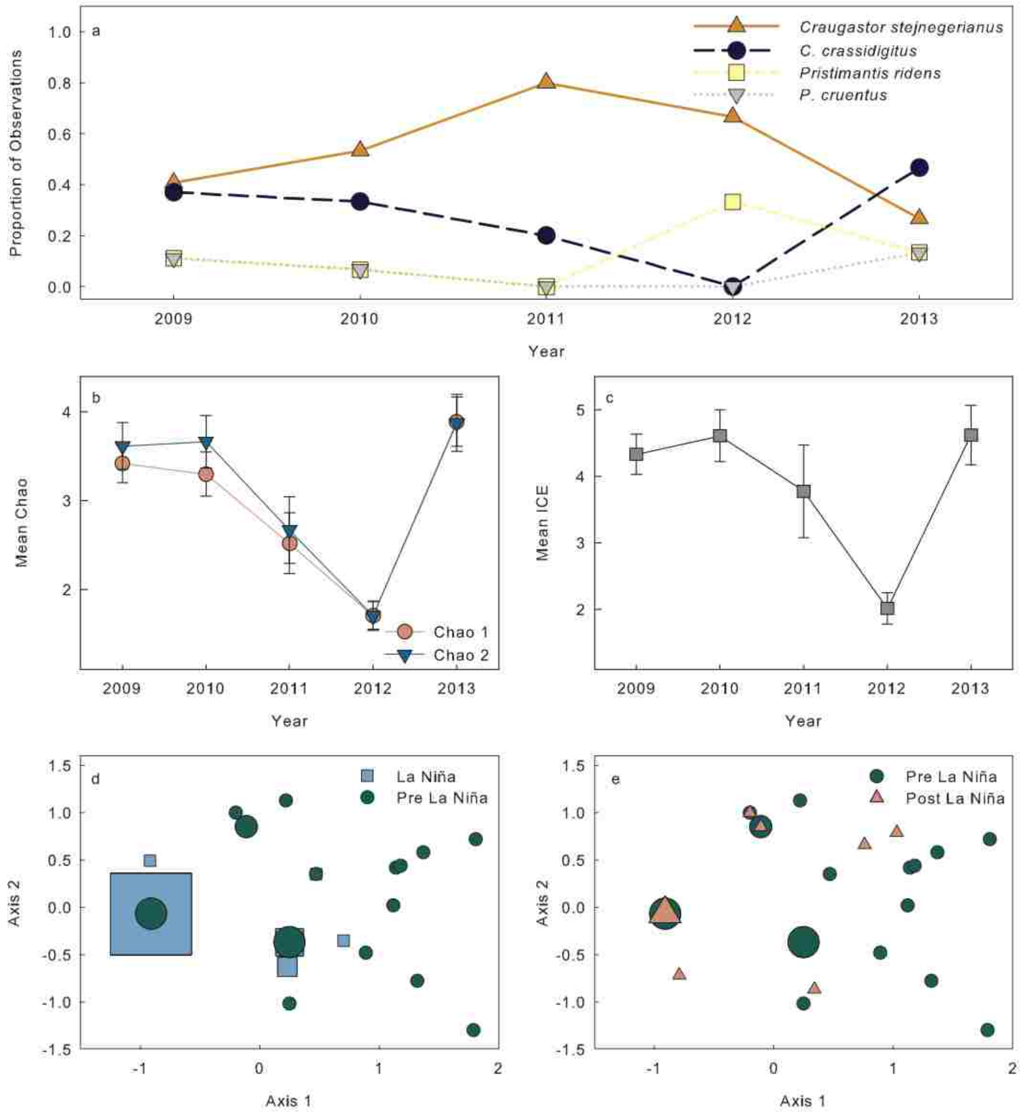

Figure 2. Terrestrial frog community changes in response to La Niña. (a) Proportion of total frog observations for each species (orange Δ= *Craugastor stejnegerianus*; navy O= *C. crassidigitus*; yellow □= *Pristimantis ridens*; grey ∇= *P. cruentus*) through time. Species diversity index plots of (c) Chao1 (peach O) and Chao 2 (blue Δ) and (d) ICE (grey □) spanning the La Niña cycle. Error bar is ±1 S.E. around mean for individual plots. (d) Ordination produced using non-metric multi-dimensional scaling (NMDS) for species composition of terrestrial frog communities in pre-La Niña (green O) versus La Niña (blue □). (e) NMDS ordination of pre-La Niña (green O) versus post-La Niña (pink Δ) frog communities. Each point in the ordinations represents frog community composition in a single plot in one year in ordination space. Size of each symbol indicates the number of plots located at that position in ordination space – for example the largest circles in panel d represent three pre-La Niña plots that were the exact same frog community composition, whereas the smallest circles are representative of one unique pre-La Niña plot.

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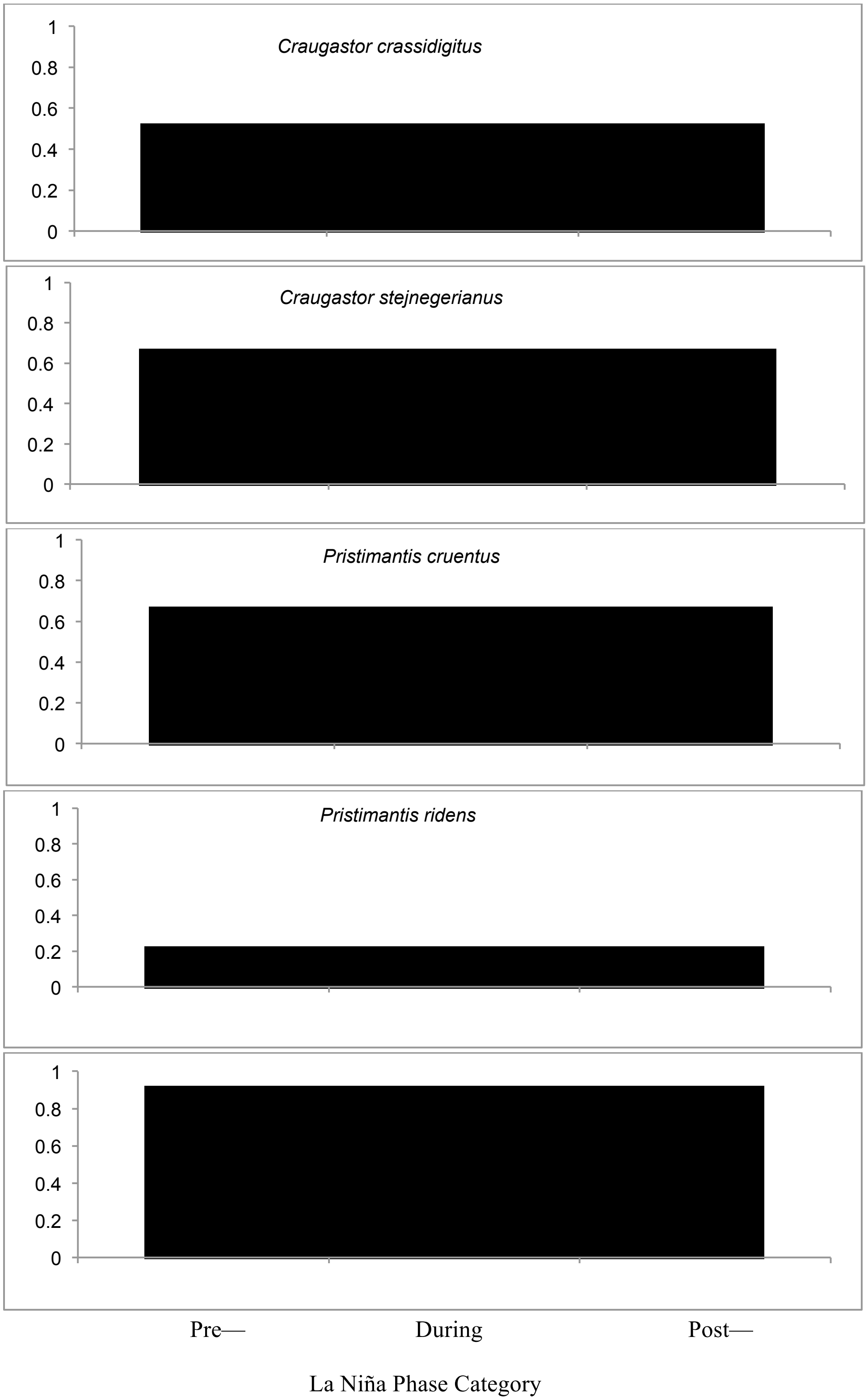

Figure 3. Percentage of plots occupied by each species for the three La Niña phase categories.

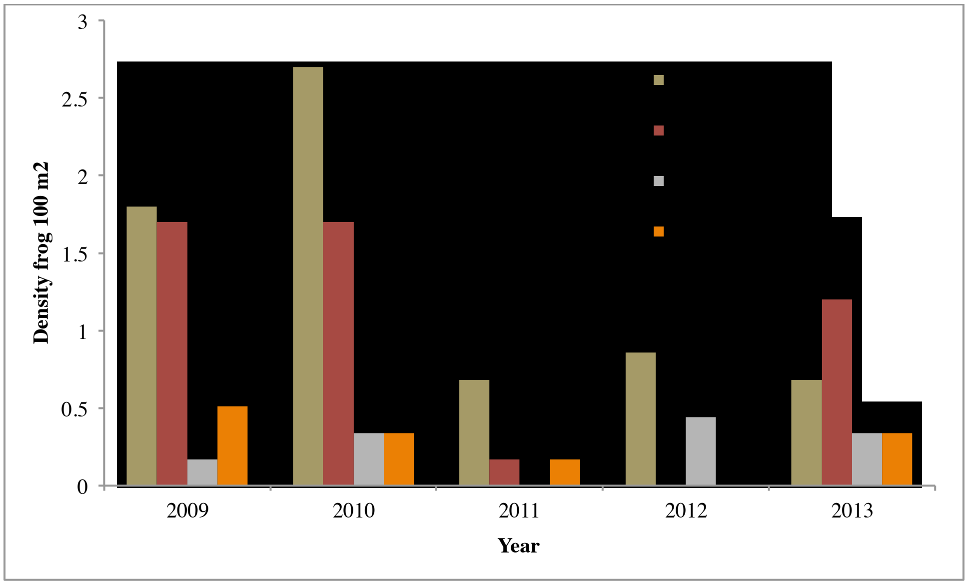

Figure 4. Annual variation in frog densities as shown from leaf litter plot sampling periods 2009-2013.

Table 1. Kruskal-Wallis results comparing species diversity indices Pre-La Niña, La Niña and Post-La Niña.

La Niña Period Result	Chao1	Chao2	ICE
Pre-Niña X La Niña			
***P*-value**	0.0004*	0.0003*	0.0140*
Z-score	-3.55	-3.56	-2.44
χ^2	12.73	12.83	6.03
La Niña X Post-La Niña			
***P*-value**	0.0005*	0.0007*	0.0274*
Z-score	3.47	3.38	2.18
χ^2	12.25	11.59	4.86
Pre- X Post-La Niña			
***P*-value**	0.012*	0.21	0.98
Z-score	2.49	1.02	0.00
χ^2	6.31	1.51	0.00

CHAPTER 4

Too dry for lizards: short-term rainfall influence on lizard microhabitat use in an experimental rainfall manipulation within a piñon-juniper woodland

Submitted and under review: Ryan MJ, IM Latella, TJ Giermakowski, H Snell, S Poe, RE Pangle, N Gehres, WT Pockman, & NG McDowell. Too dry for lizards: short-term rainfall influence on lizard microhabitat use in an experimental rainfall manipulation within a piñon-juniper woodland. Global Change Biology.

Abstract

As anthropogenic climate change increases temperature and alters rainfall patterns in terrestrial ecosystems worldwide, ectotherm populations are expected to respond by altering behavior, declining, or going locally extinct. Although changing temperatures have been shown to affect lizard behavior and microhabitat use, the role of changing rainfall patterns is not well understood. In this study, we measured lizard use of shade versus sun microhabitats for 2-years within a 5-year experimental rainfall manipulation in a piñon pine-juniper woodland in central New Mexico, USA. We used four different rainfall manipulation treatment regimes and fine-scale abiotic measurements to determine which factors predicted lizard microhabitat use. During the 5-year experiment treatment-specific mortality in piñon pine and juniper affected the quality and abundance of shaded microhabitats. We show that short-term rainfall, not temperature, best predicted the use of shade microhabitat of lizards regardless of rainfall treatment. Lizards preferentially selected shaded microhabitats during dry periods, likely as a buffer against water stress,

and this preference was consistent for treatments with either low or high tree mortality. These results confirm that shade is a critical microhabitat for lizards under different climatic regimes. Piñon pine-juniper woodlands are predicted to decline, producing a more open woodland-grassland system with less critical shade microhabitats. The loss of critical tree shade microhabitats will have cascading negative impacts on lizards that rely on tree shade to buffer against physiological stress.

Introduction

Understanding the abiotic factors that influence habitat use and behavior is crucial for predicting how animals will respond to climate change (Suttle *et al*., 2007; Smith *et al*., 2009, Scheffers *et al*., 2014). This is especially true for ectotherms, which are expected to be highly vulnerable to climate warming because environmental temperatures govern their physiology. As climate warming shifts ectotherms' thermal niches they are expected to become increasingly vulnerable to extinction (Deutsch *et al.,* 2009; Dillon *et al*., 2010; Sinervo *et al*., 2010), but the causal mechanisms driving extinction risk remain unclear (Cahill *et al*., 2012; Kearney, 2013). In ectotherms such as lizards, climate warming and thermal niche shifts have been hypothesized to increase extinction risk by reducing activity periods, which limits foraging times and fecundity, leading to extinction (Sinervo *et al*., 2010). The relationship between altered thermal niche regimes and lizard declines is complicated, and other factors such as water and food availability or species interactions may act as a proximate cause for extinction risk (Brook *et al*., 2008; Cahill *et al*., 2012). Additionally, lizards may avoid thermal stress by increasing their use of shade under future warming conditions (Kearney *et al*., 2009; Huey & Tewksbury, 2009). Because of these potentially synergistic interactions and behavioral adaptations, the thermal niche change explanation has been questioned as the driver of lizard extinctions (Kearney, 2013).

One way ectotherms can contend with increased thermal stress, especially in temperate arid and semiarid environments, is by increasing use of shade or burrow microhabitats (Kearney *et al*., 2009; Huey & Tewksbury, 2009). Microhabitat use has significant physiological consequences on lizard ecological performance (Huey, 1991), and behavioral adjustments may enhance fitness if animals have access to appropriate microhabitats as local temperatures increase with global warming (Clusella-Trullas *et al*., 2011; Callion *et al*., 2014). Changing temperatures are an obvious trigger for behavioral change, but the effects of changing rainfall patterns on ectotherm behavior and habitat use are largely unknown (Clusella-Trullas *et al*., 2011) and may elicit a similar response.

In semiarid environments, water availability is a key driver of plant productivity (Collins *et al*., 2014), and changes in this resource can negatively impact higher trophic level consumer abundance and activity (Voigt *et al.*, 2003; Suttle *et al*., 2007). Specifically, in arid regions more sporadic rainfall events can lead to temporal mismatches between available resources and consumer demand (Voigt *et al.*, 2003). Climate change, besides increasing temperatures, is intensifying the global hydrologic cycle resulting in increased intensity and frequency of extreme drought and heat events (Meehl & Tebaldi, 2004; Seager *et al*., 2007; Marvel & Bonfils, 2013). In the semi-arid western United States, water stress is exacerbated from warming temperatures and increased evapotranspiration rates leading to chronic resource alteration (Gutzler & Robbins, 2010). Decreased precipitation and changes in the frequency of precipitation events may directly result in water stress and increased mortality (Foden *et al*., 2007) and some animal or plant species may be more affected by this than increased temperatures (Crimmins *et al*., 2011).

Chronic water stress can result in bottom-up trophic effects that alter trophic interactions and behaviors, disrupting altering ecosystem and community dynamics (Voigt *et al*., 2003; Suttle *et al*., 2007; Smith *et al*., 2009; McCluney *et al*., 2012). For example, cricket and spider foraging decisions are based on water needs rather than nutrition during dry conditions, with spiders consuming more water-rich crickets, increasing predator-prey interactions when water is limiting (McCluney & Sabo, 2009). Conversely, under wet conditions both crickets and spiders decrease consumption of water rich resources, i.e. fresh leaves and crickets respectively, relative to alternative food items (McCluney & Sabo, 2009). When hydrically stressed, the lizard *Uta stansburiana* experiences reduced stamina, which may relegate individual lizards to poor microhabitats (Fox *et al*., 1981; Wilson & Havel, 1989). Furthermore, lizard reproductive output, activity patterns, and foraging consistently exhibit negative responses to a lack of rainfall in arid systems (Pianka, 1970; Ballinger, 1977).

To maintain optimal temperatures, lizards and other terrestrial ectotherms behaviorally regulate body temperature by altering their daily or seasonal use of shaded or sunny microhabitats (Huey, 1991; Adolph & Porter, 1993). Despite their dry, relatively impermeable skin, lizards must manage their water balance or risk becoming dehydrated, especially in hot and arid environments (Munsey, 1972). Symptoms of thermal stress in lizards include decreased locomotor performance, activity time, and prey acquisition; water-stressed lizards experience similar functional problems (Crowley, 1987; Wilson & Havel, 1989; Davis & DeNardo, 2009). Desiccation and heat stress are highly correlated because thermally stressed lizards cannot forage or obtain water from prey, and hydrically stressed lizards cannot properly thermoregulate (Crowley, 1987). Lizards balance the physiological interaction between thermal stress and water loss by shuttling across warm exposed and cool shaded microhabitat gradients (Stevenson, 1985; Huey & Tewksbury, 2009). For this to be an effective strategy there must be stability in the abundance and quality of available microhabitats (Kearney, 2013).

Piñon pine-juniper woodland is the most common forest type in the southwestern United States, covering more than 36 million acres (Shaw *et al*., 2005). It also is one of the most threatened forest types from direct and indirect climate change factors (Gutzler & Robbins, 2010; Gaylord *et al*., 2013). Over the last century, warming and drying trends across the southwestern United States have dramatically altered forest structure, and these climatic stressors are expected to become more severe (Anderegg *et al*., 2012; Williams *et al*., 2013). Both piñon pine and juniper are vulnerable to drought stress, but piñon pine are experiencing disproportionately higher mortality rates than juniper trees (Gaylord et al., 2013). This drought vulnerability and tree mortality is likely to lead to an ecological state transition from woodlands to more simplified juniper-grassland or grassland habitats (Allen & Breshears, 1998; Breshears *et al*., 2005; Collins *et al*., 2014). Because piñon pine-juniper woodlands provide a structurally heterogeneous mosaic of widely spaced and unevenly distributed shaded microhabitats, reductions in tree cover will remove the relatively cool and humid physiological shade refuge available for ectotherms such as lizards (Chen *et al*., 1999; Gutzler & Robbins, 2010; Kearney, 2013).

Although there is a rich body of work on lizard responses to increased temperatures (e.g. Sinervo *et al*., 2010; Huey *et al*., 2012; Kearney *et al*., 2013), little is known about lizard responses to climate change and water stress. Furthermore, studies of lizard responses to climate change and increased temperatures typically rely on broad spatial and temporal scales (Kearney *et al*., 2009; Sinervo *et al*., 2010; Clusella-Trullas *et al*., 2011). For example, it is standard practice to use coarse climatic layers from WORLDCLIM at 10-arc minute resolution in climate change studies (e.g. Hannah *et al*., 2014). While informative, relying on broad scale climatic data can create a mismatch between local abiotic conditions, microhabitat conditions, and expected organismal response in situ (Potter *et al*., 2013). Therefore, relating fine-scale subhourly abiotic conditions which animals are exposed to in situ is likely to be important for understanding biological responses to future climate change (Hannah *et al*., 2014).

Field experiments that manipulate rainfall and temperature are ideal for testing the effects of climate change on microhabitat use of free ranging ectotherms (e.g. Suttle *et al*., 2007; Walther, 2007). In this study we used four ecosystem level treatments where rainfall and temperature were manipulated in a piñon pine-juniper woodland in central New Mexico (Pangle *et al*., 2012) to assess the daily microhabitat use of a lizard species. The study species, *Aspidoscelis exsanguis*, is a thermoregulator that shuttles between both open and shaded microhabitats while actively foraging (Echternacht, 1967); but their daily activity is hydrically costly and lizards may expend up to 63% of their water mass while active (Bowker, 1993). Our experimental design allowed us to relate microhabitat use to real-time subhourly temperatures and rainfall experienced by hydrically stressed free-living lizards. We asked which abiotic elements, ground temperature or short-term rainfall, best-predicted *A. exsanguis'* microhabitat use within each treatment type. We predicted that lizards would use tree shade microhabitats more than exposed sun microhabitats in the warmer, drier treatments than in the cooler, wetter treatments. Because high tree mortality and canopy dieback have been previously reported from this study system (Gaylord *et al.,* 2013), the reduction of tree shade may have a cascading effect on lizards' ability to buffer against future climate change impacts in piñon pine-juniper woodlands (Kearney, 2013).

Material and Methods

Study Site

This study was conducted at the Sevilleta National Wildlife Refuge LTER on the eastern slope of the Los Pinos Mountains, Socorro County, New Mexico, United States (34°23′11″ N, 106°31′46″ W; elevation 1911 m). Two species of trees were dominant at the study site, piñon pine (*Pinus edulis*) and oneseed juniper (*Juniperus monosperma*). Typically, these trees occur in patchy clumps (2-10 m apart) in a matrix of bare ground, bunch grasses, cacti, and small shrubs between trees. A nearby Sevilleta LTER weather station (Cerro Montoso #42; http://sev.lternet.edu/) indicated that the 20-year mean (1989-2009) annual precipitation was 362.7 mm/year, with a mean annual temperature of 12.7 °C (maximum mean monthly of 31.0 °C in July; minimum mean monthly -3.3 °C in December). The site is strongly influenced by seasonal monsoons that occur between July and September (Pangle *et al*., 2012).

Study Design and Experimental Treatments

Study plots were dispersed over 25 ha in a piñon-juniper woodland. Rainfall manipulation treatments began in 2007 and continued after lizard sampling during 2011 and 2012. The study system is comprised of four rainfall treatments with three replicates per treatment, for a total of 12 experimental plots: 1) ambient (no cover, receives all ambient rainfall); 2) irrigation (received six simulated 19 mm rainfall events between April and October); 3) drought (partially covered with transparent polymer troughs 1 m above the surface to remove ~45% of ambient rainfall from the plot); 4) cover control (covered with transparent polymer that is domed to allow ambient rainfall to reach the ground). Plots were 1600 m^2 (two drought plots are on adjacent slopes, treating 3200 m^2)

and roughly square, with boundaries delineated by treatment structures or flagging. We considered the adjacent plots as a single 3200 m^2 plot, even though it was treated as two separate 1600 m^2 plots in the original design (Pangle *et al*., 2012). Additional details of the study site construction and design for rainfall manipulation are provided in Pangle *et al*. (2012). Plots were not fenced and lizards could move freely in and out of plots.

By 2011, the fourth year of the rainfall manipulation study, significant tree mortality and canopy die-back had occurred in the drought treatments, particularly on hill slopes, and was attributed to a combination of simulated drought stress and insect attacks within the study plots (Gaylord *et al.,* 2013). For example, by 2010, 70% of piñon pines in the drought plots experienced whole-tree mortality, while juniper trees experienced up to 50% cumulative canopy browning or dieback. Within the other treatments (ambient, cover control and irrigation), piñon pines experienced 10% mortality and juniper canopy cover was reduced by 15-20% due to naturally occurring drought conditions (Gaylord *et al*., 2013).

Abiotic variables

To calculate the short-term rainfall prior to sampling, we used the cumulative ambient rainfall from the previous 7-days from a weather station located on-site (Pangle *et al*., 2012). For the irrigation treatment plots we included any simulated 19 mm rainfall events to the 7-day ambient rainfall amount and for drought treatment plots we reduced ambient rainfall by 45%. We used mean and maximum air and ground temperature measurements from 630 hr to 1230 hr for the dates we recorded lizard behaviors. We used this time range for temperature measurements because it covered the fluctuation in temperatures that lizards were exposed to immediately prior to- and during our lizard sampling. We obtained, at 15-minute intervals, soil temperature measurements from sensors buried 5 cm deep and air temperature from sensors 10 cm above the ground (see Pangle *et al*., 2012). Temperature sensors were placed under tree canopies and in exposed intercanopy areas allowing us to calculate 6-hour mean soil temperature for each plot and treatment and mean temperature in shade and sun microhabitats. We used the temperature measurement from 1230 hrs for daily mean maximum soil temperature. Datasets of the abiotic variables can be accessed from the LTER Portal (Pockman & McDowell, 2014).

Drought and cover control treatments (i.e., with polymer covers) displayed increased soil and air temperatures of 1-4 °C compared to non-covered treatments (Pangle *et al*., 2012), which is within the temperature increase predicted by year 2100 (IPCC, 2007). This warming artifact of the plot design allowed us to examine lizard microhabitat use under different thermal and precipitation regimes that include current conditions, warmer and drier conditions, and warmer and wetter conditions.

Lizard biology and sampling

Unlike many whiptail lizards, *A. exsanguis* is not wary of people and is easily observed at a close distance without disrupting its behavior (Echternacht, 1967). Seasonal activity of *A. exsanguis* occurs from April to September, and daily lizard activity is governed by ground temperatures and typically begins around 0630-0700 hr when ground temperatures approach 26 °C and ceases mid-day when temperatures approach 50 °C (Echternacht, 1967). To maximize lizard observations daily sampling began between 0700 hr-0800 hr and ended no later than 1200 hr. We sampled plots weekly starting the last week of May and continued through the first week of August in 2011 and 2012, covering most of the species' seasonal active period. In 2011 each plot was sampled 10 times and in 2012 plots were sampled 14 times. We slowly walked and scanned the ground to record lizard microhabitat use within plot boundaries. We used short-focus binoculars to minimize disturbance as we identified lizards to species and observed behavior. For each observation we recorded: 1) time of observation; 2) microhabitat (open or under tree); 3) sun or shade; and 4) behavior (active foraging, digging or scratching, basking). We define microhabitat use as the specific patch of habitat, shade or sun, where a lizard was observed (Anderson, 2007).

Analyses

We used ANOVA to compare the mean abiotic variables between 2011 and 2012 to determine if there were significant differences between years. We found no difference in abiotic conditions between years (S Table 1) and therefore analyzed 2011 and 2012 together for all further analyses. We used ANOVA to determine if mean soil and air temperatures differed among treatments and between shade and sun microhabitats among treatments. We used ANOVA to test if the mean percentage of green canopy cover of focal trees (Gaylord *et al*., 2013) had changed between 2007 and 2012 for each treatment. This was done to determine if the long-term experimental treatment affected canopy cover by the time of our lizard sampling. Green canopy cover change was recorded for 32 trees in the ambient treatment, 30 in cover control, 42 in drought, and 34 in irrigation treatments.

We used a generalized regression with a zero-inflated poisson distribution to test whether the number of lizard observations differed by treatment type. This approach is appropriate for our data because we had sampling periods with zero observation and the zero-inflated poisson allows for overdispersion when observations of zero are part of the dataset (Crawley, 2013). Because treatment type is defined by rainfall amount, we only used the number of observations per sampling period for this analysis.

We analyzed the frequency of lizards observed in shade or sun as a binomial response with logistic regression to test the null hypotheses of no relationship between short-term rainfall and/or 6-hour mean and 1230hr maximum temperatures and use of shade versus sun habitats for each treatment (Crawley, 2013). This approach allowed us to correspond microhabitat use observations with specific real-time abiotic variables experienced by the lizards while active. We first ran the logistic regression with an interaction term between short-term rainfall x 6-hour mean and 1230hr maximum soil temperatures. We used a Wald test to determine if the use of an interaction term is justified, where a non-significant Wald test indicates lack of evidence for an interaction and that a simpler model with no interaction should be used (Crawley, 2013). Based on the logistic regression results with the interaction term we then used a simple logistic regression model with rainfall as the only independent variable. All analyses were done in JMP-9 (SAS, 2010).

We used Bowker's (1993) linear regression equation $(9.4*10^{-9})$ $(1.67^{X})+2.34$; (X = soil temperature °C) to estimate total water loss for *A. exsanguis* over the 6-hour morning active period (i.e. 0630 to 1230 hr). Bowker (1993) calculated weight loss (grams) per hour and assumed that weight loss represented water loss by the lizard. Since we do not have lizard field body temperature measurements we use the mean 6-hour ground temperature measurements as a proxy (e.g. Echternacht, 1967; Bowker, 1993). We calculated water loss as grams/hour (g-h) for shade and sun habitats during wet (> 4 mm rainfall previous 7-days) and dry periods (< 4mm rainfall previous 7-days).

Results

Between 2011 and 2012, there was no significant difference in mean air temperature (ANOVA: ambient: $P = 0.43$; $F = 2.46_{1,68}$; cover control: $P = 0.12$; $F = 0.79_{1,70}$; drought: $P = 0.09$, $F = 2.83_{1,70}$; irrigation $P = 0.06$; $F = 3.94_{1,70}$) or soil temperature (ANOVA: ambient: $P = 0.37$; $F = 0.79_{1,68}$; cover control: $P = 0.08$; $F = 3.14_{1,70}$; drought: $P = 0.16$, $F = 1.94_{1,70}$; irrigation $P = 0.33$; $F = 0.95_{1,70}$). Ambient and irrigation plots experienced lower temperatures than cover control and drought plots (Fig. 1). For each treatment maximum soil temperatures were significantly cooler in the shade compared to the sun habitats (Fig, 2; ANOVA: ambient: $P = 0.0001$; $F = 360.7_{1,138}$; cover control: $P = 0.0001$; $F = 740.0_{1,142}$; drought: $P = 0.0001$, $F = 434.0_{1,142}$; irrigation $P = 0.0001$; $F = 328.1_{1,142}$.). Drought treatments showed the largest difference between shade and sun temperatures and irrigation showed the smallest differences, with ambient and cover control being intermediate. The irrigation treatment received the highest amount of rainfall, followed by ambient and cover control, and drought had the least amount of rainfall.

We had a total of 460 lizard observations (208 in 2011; 252 in 2012) across all treatments. For 2011 and 2012 combined we made 103 observations in the ambient, 63 in cover control, 94 in drought, and 200 in irrigation treatments. Lizard observations tended to peak following short-term rainfall pulse events (Fig. 3). Our overall generalized zero-inflated poisson regression model indicates an effect of treatment on the number of lizard observations ($P = 0.0001$, $\chi^2 = 41.12_{3,288}$). The treatment-level results from the generalized zero-inflated poisson regression model indicate that the irrigation treatment had significantly more lizard observations than all other treatments (ambient: $P = 0.012$, *SE* = 1.30, χ^2 = 6.3, estimate = -3.27; cover control *P* = 0.0001, *SE* = 1.73, χ^2 = 32.93, estimate -9.98; drought: *P* = 0.0001, *SE* = 1.45, χ^2 = 18.56, estimate -6.25).

During dry periods, lizards had a higher likelihood of being observed in tree shade whereas following a rainfall pulse event lizards were more likely to be found in the sun, irrespective of treatment. The logistic regression model incorporating rainfall, mean soil temperature and the interaction term showed that short-term rainfall was the strongest predictor of lizard microhabitat use and soil temperature was a nonsignificant predictor in all treatments (Table 1). The simplified, single variable rainfall logistic regression models showed the same results; rainfall better predicts microhabitat use (ambient: *P* = 0.0001, *SE* = 0.03, χ^2 = 10.72, estimate = -0.11; cover control *P* = 0.013, *SE* = 0.05, χ^2 = 6.11, estimate -0.12; drought: *P* = 0.0024, *SE* = 0.10, χ^2 = 9.19, estimate -0.31; irrigation *P* = 0.0034, *SE* = 0.01, χ^2 = 8.57, estimate -0.05). The logistic regression model with all treatments combined was also significant for short-term rainfall predicting habitat use (*P* = 0.0001, *SE* = 0.012, χ^2 = 22.10, estimate -0.05; Fig 4). Thus, there was a strong effect of rainfall and no effect of temperature on shade vs. sun habitat use, even for the warmest and driest treatments.

Since rainfall manipulation started in 2007, the mean percentage of green canopy cover has decreased, regardless of treatment type (Fig 5). Between 2007 and 2012 green canopy cover in the ambient treatments decreased by 25% (ANOVA: *P* = 0.0001; *F* = $35.68_{1,61}$); cover control decreased by 30% (*P* = 0.0001; *F* = $68.20_{1,58}$); drought decreased by 68.9% (*P* = 0.0001, *F* = $125.85_{1,71}$), and irrigation by 24.1% (*P* = 0.0001; *F* = $33.10_{1,63}$).

The water loss proxy model predicts lizard water loss should be greater in the sun compared to shade, and this difference was accentuated during dry periods (Fig. 6). The total estimated lizard water loss for the 6-hour morning active period differed significantly between shade and sun habitats during dry (ANOVA: $P = 0.0001$, $F = 47.38_{1,370}$), and wet periods (ANOVA: $P = 0.0001$, $F = 24.77_{1,196}$) for all treatments combined.

Discussion

Forecasts of future impacts of climate change on ectotherms such as lizards must take both temperature and rainfall into account (e.g. Clusella-Trullas *et al*., 2011; Lovich *et al*., 2014) and also consider fine-grained variation in abiotic conditions (Hannah *et al*., 2014). By studying lizard microhabitat use within the framework of an established large-scale climate manipulation study, we were able to investigate how real-time, subhourly temperature and rainfall influences free-living lizard microhabitat use under different rainfall treatments. Detailed studies of microhabitat use such as this are sorely needed in the climate change field (Bernardo, 2014).

Our most striking finding is that short-term rainfall, rather than temperature, influenced daily lizard microhabitat use, even in the warmest drought treatments. The greater effect of rainfall relative to temperature on microhabitat use contradicts previous findings of lizard responses to climate change (Kearney *et al*., 2009). During periods with low rainfall, lizards were more often observed in shade than sun and during periods with >4 mm of rainfall lizards were more often observed in the sun (Fig. 4). These findings reinforce the complexity of predicting species responses to climate change and confirm that fine scale autecological-environmental interactions are needed to best predict individual species responses (Clusella-Trullas *et al*., 2011; Hannah *et al*., 2014). They further have implications for the future population health of ectotherms. It is important to emphasize that, according to our findings, any behavioral response to either rainfall or temperature change depends on the availability of shade microhabitat refugia. Much of the southwestern United States is experiencing extreme droughts and long-term drying trends that is causing high rates of tree mortality (Breshears *et al*., 2005; Williams *et al*., 2013), which should have cascading, deleterious impacts on shade using lizards (Kearney, 2013; Clusella-Trullas & Chown, 2014).

We propose that two drivers explain the rainfall-associated shift in lizard microhabitat use. First, lizards may simultaneously minimize water loss and thermal stress when active in the shade during harsh dry periods. Rate of evaporative water loss in lizards is positively associated with both arid conditions and higher temperatures (Claussen, 1967; Munsey, 1972). Lizards near their dehydration threshold prefer lower temperatures than hydrated animals (Crowley, 1987; Angilleta, 2011); and the behavioral solution to this dilemma may be to move from sun to shade, which can decrease body temperature by 5°C (Stevenson, 1985). Bowker (1993) found water loss in *A. exsanguis* increased exponentially as substrate temperature increased beyond 37°C, and he suggests that water may be the most important factor limiting activity and determining microhabitat use in these lizards. In our study, the use of shade microhabitats during dry periods supported Bowker's assertion that water loss determines *A. exsanguis* behavior. This result also fits with Stevenson's (1985) behavioral solution of lizards using shade, which may be up to 8.5°C cooler than sunny microhabitat (Fig. 1), which can aid in water conservation during dry periods (Fig. 6). The use of shade microhabitat during dry periods allows *A. exsanguis* to simultaneously remain active and foraging while conserving water in shade tree island refugia.

Second, trophic level species interactions may influence lizard microhabitat use as they either respond to aboveground arthropod prey distribution or switch to alternative below ground prey during dry periods. Water availability has a positive effect on arthropods in arid environments and under wetter conditions more aboveground insect prey should be available to lizards (Shepherd *et al*., 2002; Stone *et al*., 2010). At a short-term, daily time-scale, Schowalter *et al*. (1999) observed an increase in arthropod abundance and diversity following experimental watering in a creosote-grassland, indicating that arthropods respond quickly to moisture pulses. Trotter *et al*. (2008) found arthropod abundances and diversity in piñon pine-juniper woodlands decreased when drought stresses were high. The concomitant ebb and flow of rainfall pulses can have trophic cascade consequences (Lensing & Wise, 2006) that ultimately influence lizard foraging and their prey diversity (e.g. McCluney & Sabo 2009). Both trophic interactions and hydric stress may be driving our observed patterns, and at this point we cannot disentangle their effects.

Increased temperatures have been identified as the greatest threat to lizard populations (Sinervo *et al*., 2010; Huey *et al*., 2010), and are predicted to influence lizard microhabitat use (Kearney *et al*., 2009). The effects of extreme temperatures may be offset when lizards switch microhabitat use during harsh thermal conditions (Kearney *et al*., 2009) or following sporadic rainfall events. Our results indicate that the soil temperatures lizards experienced while active had no observable effect on *A. exsanguis'* preference for shade or sun microhabitats. We hypothesize that the lack of a temperature effect is rooted in the thermal biology of *A. exsanguis*. We do not have field body temperatures for our lizards, but *A. exsanguis* maintains a field body temperature of 38.5 °C at ground temperatures of 41.7 °C (Schall, 1977; Bowker, 1993). During our daily sampling periods mean ground temperatures were within the normal active range of *A. exsanguis,* even under the warmest drought and cover control treatments (Fig 1). The lack of an effect in these warmer treatments was surprising and suggests that *A. exsanguis* may not be very vulnerable to future warming temperatures if rainfall events remain stable and shaded microhabitats remain part of the landscape.

Shifting microhabitat use is frequently cited as a strategy for countering the effects of climate change (Scheffers *et al*., 2014). However we note that any behavioral response to either rainfall or temperature change depends on the availability of suitable shade refugia that may themselves be affected by climate change. In particular, in arid or semiarid environments it is important to account for the concomitant impacts of climate change on trees, which provide critical shade microhabitats (Allen & Breshears, 1998; Breshears *et al*., 2005; Kearney *et al*., 2013). The decline of piñon pine-juniper woodlands or the decrease in canopy cover quality (i.e. green to brown canopy cover), poses serious dangers to animals that rely on this habitat. We observed just such a decline in our study plots: there was a significant decrease in green canopy cover for all treatments between 2007 and 2012, as well as high tree mortality (Fig. 5; Gaylord *et al*., 2013). Drought, fires, and bark beetle outbreaks have reduced the coverage of piñon-juniper woodlands over the last few decades driving a shift to juniper and/or grassland dominated systems (Breshears *et al*., 2005; Williams *et al*., 2013). The loss of tree cover and decrease in canopy quality in this system may have severe consequences for *A. exsanguis* and other ectotherms even beyond the loss of protective microhabitat. For example, drought-stressed piñon pine support lower arthropod abundance and diversity than non-drought stressed trees (Stone *et al*., 2010). This pattern suggests a bottom-up trophic cascade in this system.

During the course of sampling we observed many behaviors of *A. exsanguis* that helped inform our interpretations. Foraging and microhabitat behaviors of *A. exsanguis* fluctuated with rainfall pulses, with foraging area expanding following rainfall pulses indicated by roughly equal sun or shade, or more sun observations of lizards following pulses of short-term rainfall (Fig 3). Over the course of our sampling lizards moved quickly and directly between the 3-10 meters separating tree-shade islands during dry periods. During dry periods, *A. exsanguis* foraged by scratching and digging in the friable needle litter under tree canopies and fed on various below ground invertebrate larvae and smaller prey including termites. During wetter periods lizards expanded their foraging area to sun microhabitats and foraging behaviors switched from scratching and digging to actively searching for aboveground prey. While foraging in sun microhabitats, we observed feeding on aboveground prey such as moths, beetles, grasshoppers and cicadas. As conditions became drier, lizards once again became more common in the shade, emphasizing the role of rainfall, not just on microhabitat use, but also on the total area available for food acquisition. The shifts in microhabitat and foraging behaviors provided evidence that rainfall strongly affected where and how *A. exsanguis* located prey. Furthermore, lizards were active for at least 5 hours per day, with no evidence of restricted activity times in any treatment.

Our findings of short-term rainfall driven microhabitat use can likely be extrapolated to other ectotherms that occur in piñon pine-juniper woodlands, such as snakes and arthropods. Most ectotherms must cope with the same physiological stresses associated with warmer temperatures and drought (Deutsch *et al*., 2009; Dillon *et al*., 2010). Similar to our lizard results, many invertebrates exhibit similar use of shade microhabitats to avoid stressful abiotic conditions (Shepherd *et al*., 2002; Stone *et al*., 2010). The loss of piñon pine and juniper trees due to climatic stresses will result in fewer and more widely spaced shade islands. In the short term, animals in this system will have to contend with several problems including locating the increasingly rare shade islands and possible increases in competition. However, the likely consequence of an eventual shift to a juniper-grassland or grassland will be the extirpation of the current lizard species that depend on the current heterogeneous piñon pine-juniper habitat mosaic.

Acknowledgments

We thank the following individuals for assistance in coordinating and collecting field data: Brad Truett, Hannah Marti, Aja King, Krista Gibboney, Eric Schaad, Jennifer Johnson, Rina Ouellette, and Amaris Swann. Scott Collins, Megan Workman, and Joseph Cook provided valuable feedback on early drafts of this manuscript. We thank the U.S. Fish and Wildlife Service and Jon Erz for issuing research permits and providing access to the Sevilleta National Wildlife Refuge. This project was supported by the National Science Foundation's Graduate Research Fellowship Program to Mason J Ryan; by the Department of Energy's Office of Science (BER) via awards to Nate McDowell and Will Pockman; and by the Sevilleta LTER (supported by NSF DEB-0620482) and UNM-Sevilleta Field Station.

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Figures and Tables

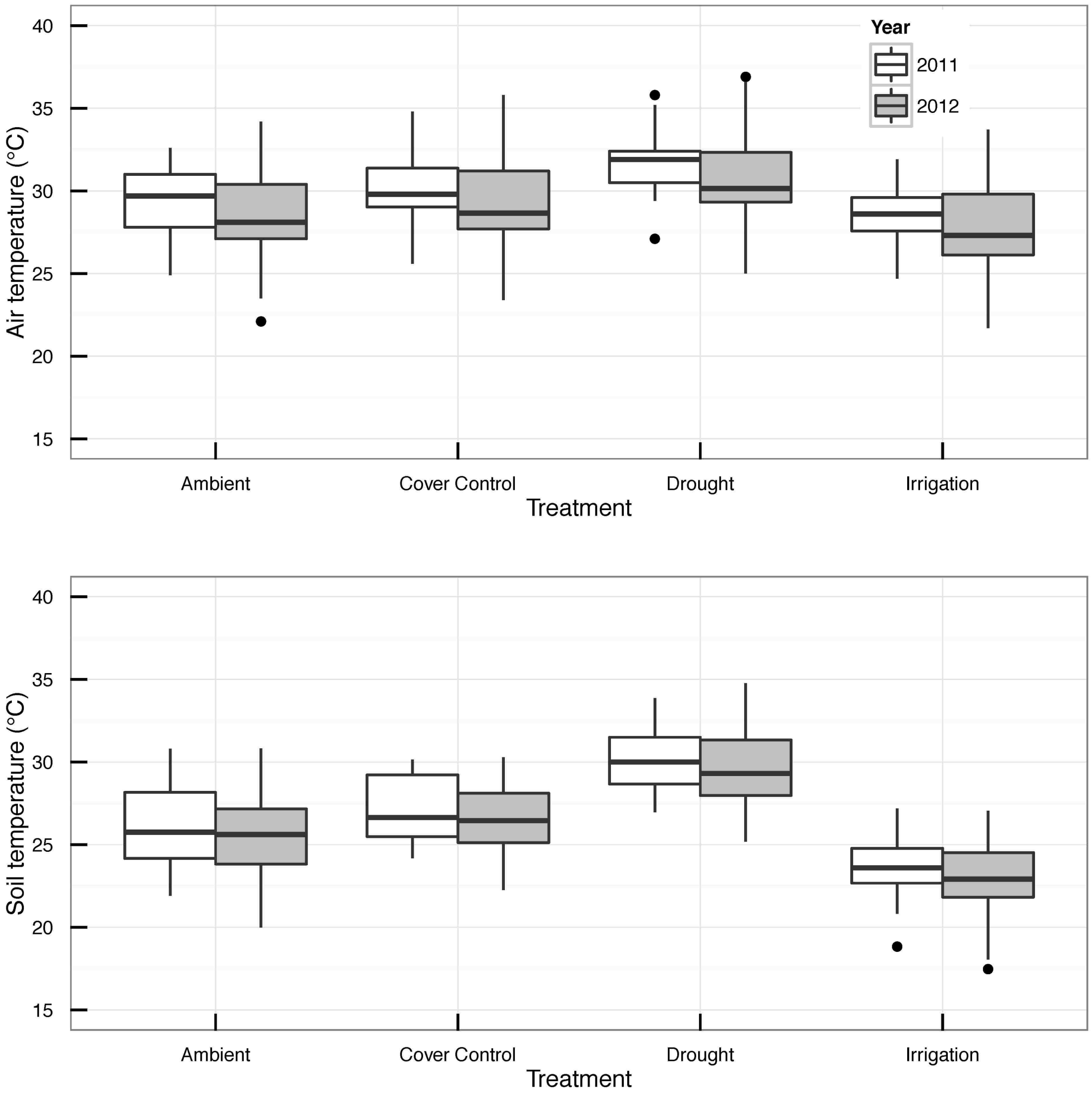

Fig. 1 Box plots of mean air and ground temperatures for each treatment type during the months (May – August) of lizard sampling 2011 and 2012.

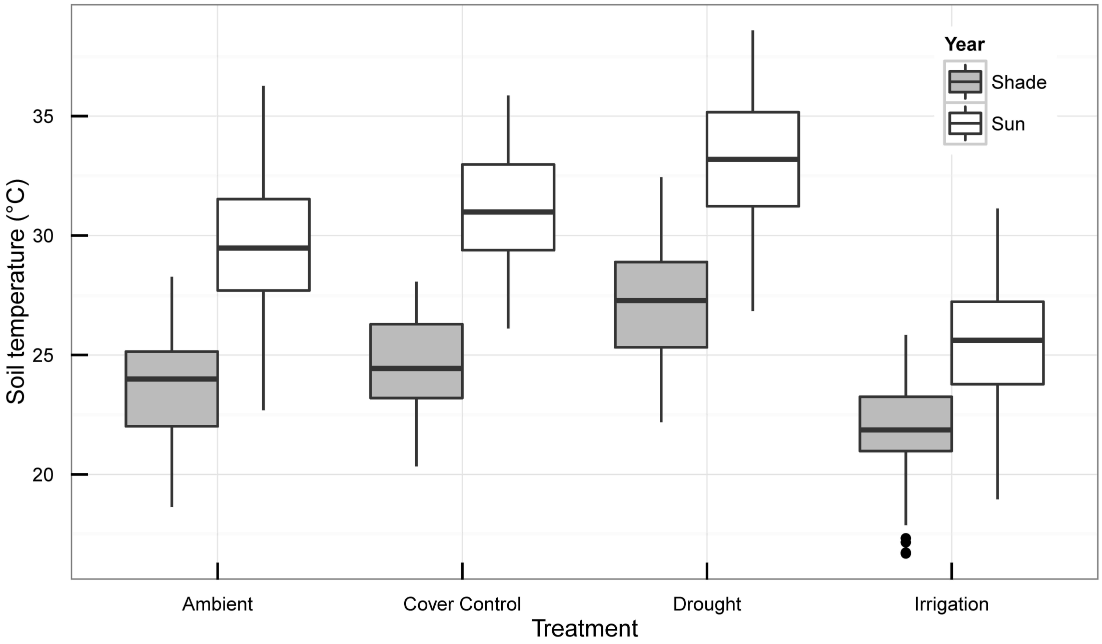

Fig. 2 Box plots of mean 6-hour soil temperatures in shade and sun microhabitats for each treatment type. Soil temperatures were significantly lower in shade across all treatments. The 6-hour time period covers the time of day lizards were active and represents the conditions lizards were exposed to.

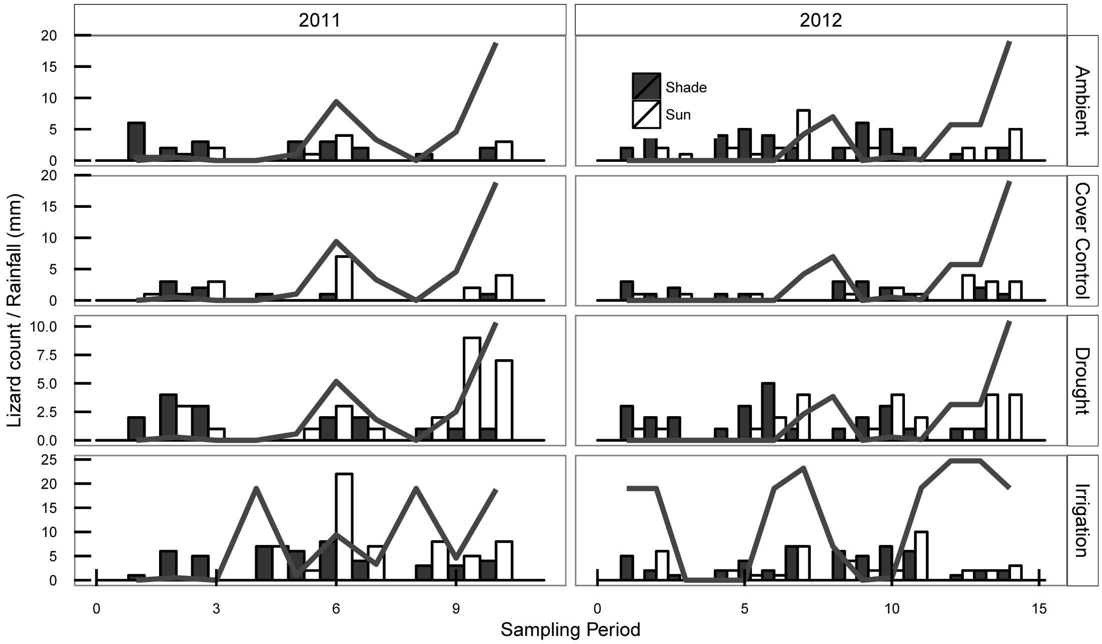

Fig. 3 Frequency of shade or sun lizard observations and short-term rainfall (solid line) for each treatment and sampling period in 2011 and 2012.

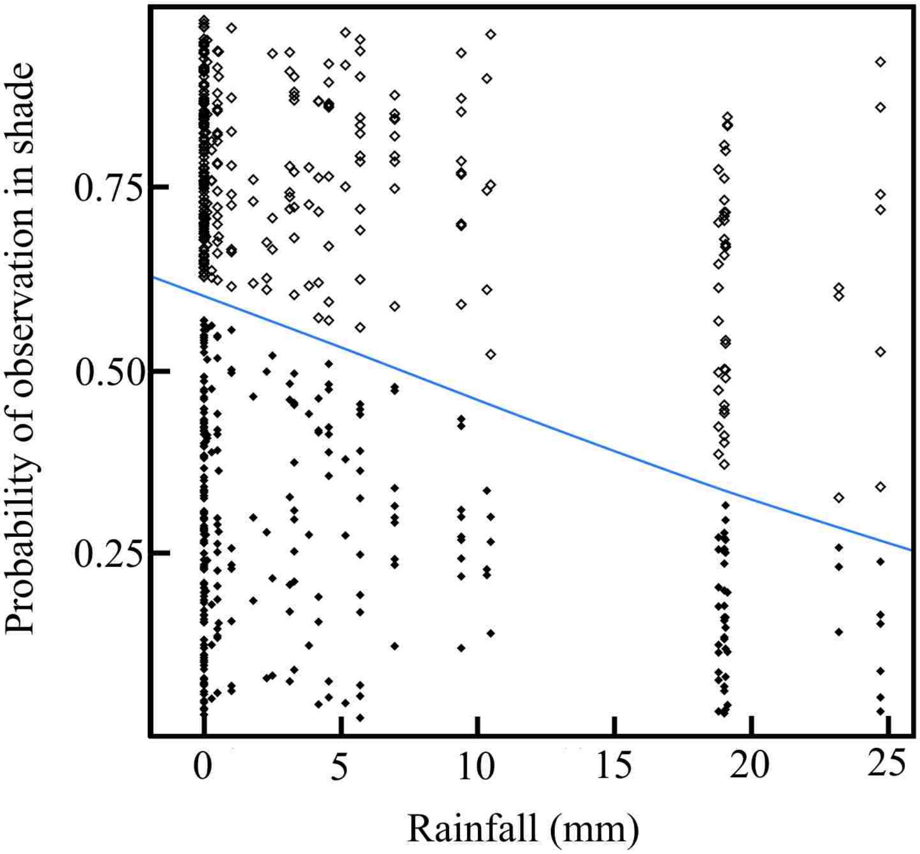

Fig. 4. Logistic regression plot of short-term rainfall by probability of observation in shade (open circles = sun; black circles = shade) for all treatments combined. Points represent observations from sampling periods and short-term rainfall. See text for logistic regression results.

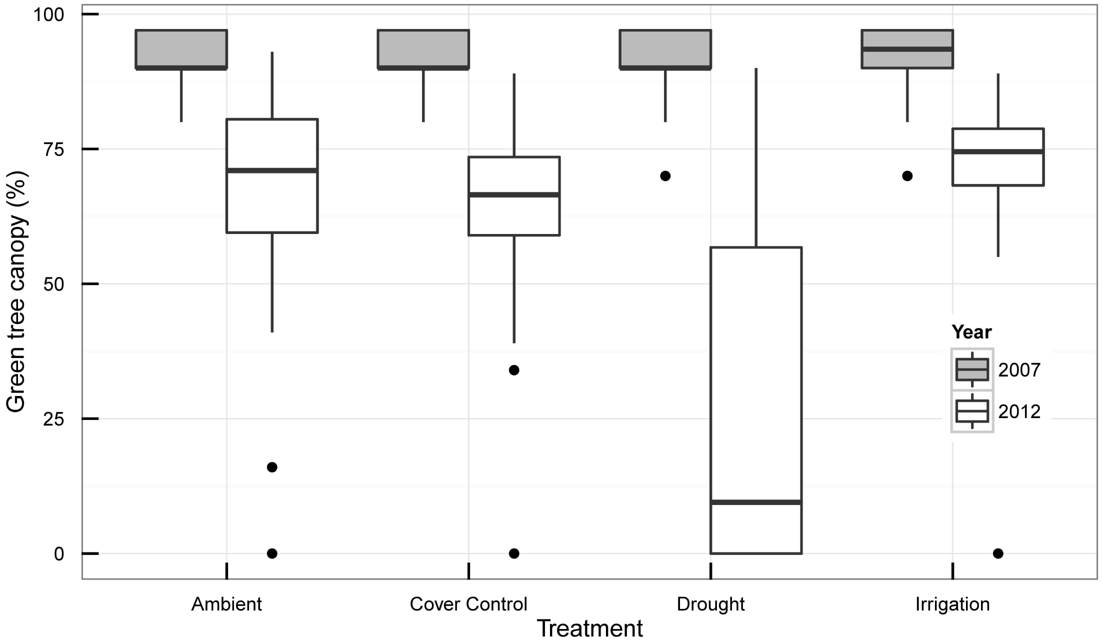

Fig. 5 Box plots of mean percent change in live, green canopy cover between 2007 (start of the rainfall manipulation) and 2012 (last year of lizard sampling) for each treatment. Percent of green canopy cover comes from focal trees monitored annually within the study plots. There was a significant decrease in green canopy cover for all treatments, and the drought plot showed the greatest change.

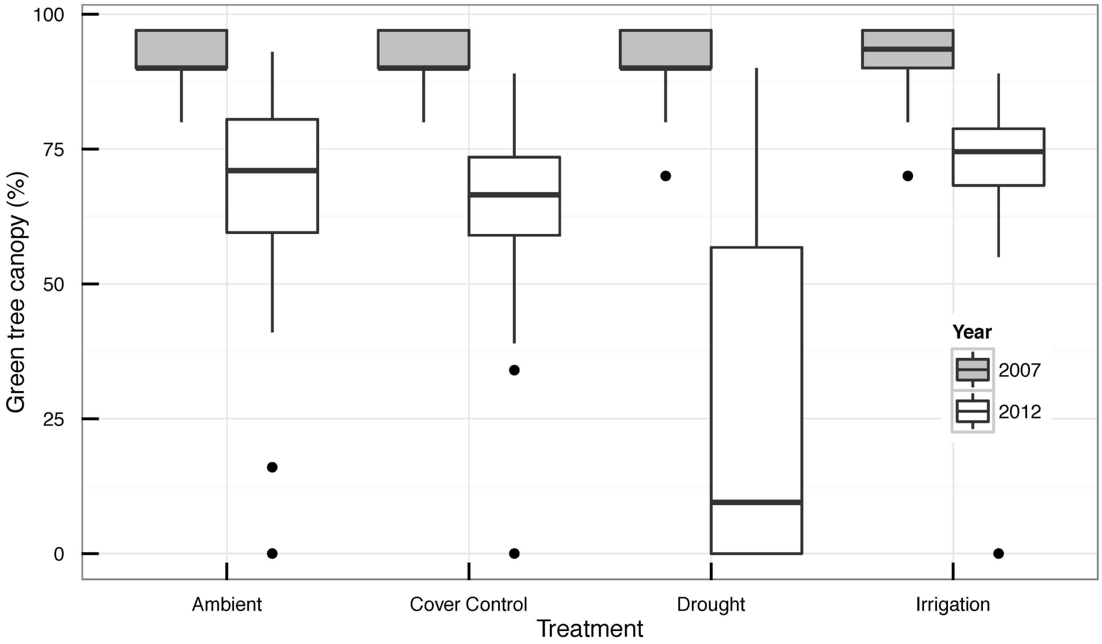

Fig. 6 Box plots of estimated lizard water loss (mg of water/hour) within each treatment, and shade or sun microhabitats. The model predicts lizard water loss to be greatest during dry periods while lizards are in the sun, and that water loss is least when in the shade.

Table 1 Logistic Regression model results of shade/sun habitat use by rainfall and mean maximum soil temperatures at 1230 hrs and 6-hour mean soil temperature. Wald test determined that adding a rainfall*temperature parameter was uninformative and overparameterized the model.

Treatment	***P***	$\chi^2_{df,\,n}$	**Estimate ± *SE***	**Wald test *P***
Tsoil @1230hrs				
Ambient				
Whole Model	0.001*	$12.56_{2,102}$		
Rainfall	0.001*	10.64	-0.13±0.04	0.0004*
TsoilMax	0.15	2.07	-0.13±0.09	0.15
Cover Control				
Whole Model	0.007*	$9.71_{2,63}$		
Rainfall	0.03*	3.89	-0.10±0.05	0.04*
TsoilMax	0.17	1.84	0.16±0.12	0.17
Drought				
Whole Model	0.0003*	$16.55_{3,94}$		
Rainfall	0.0064*	7.42	-0.28±0.10	0.008*
TsoilMax	0.25	1.29	0.09±0.08	0.25
Irrigation				
Whole Model	0.009*	$9.30_{3,200}$		
Rainfall	0.01*	6.50	-0.04±0.01	0.009*

TsoilMax	0.50	0.45	0.04±0.07	0.49
$\bar{x}$ **Tsoil 6-hour**				
Ambient				
Whole Model	0.002*	$11.92_{2,102}$		
Rainfall	0.001*	9.93	-0.12 ± 0.03	0.001*
Tsoil $\bar{x}$	0.22	1.45	-0.12 ± 0.1	0.22
Cover Control				
Whole Model	0.01*	$9.14_{2,63}$		
Rainfall	0.03*	4.47	-0.11±0.05	0.03*
Tsoil $\bar{x}$	0.25	1.31	0.17±0.15	0.25
Drought				
Whole Model	0.0005*	$15.33_{3,94}$		
Rainfall	0.002*	9.30	-0.32±0.10	0.002*
Tsoil $\bar{x}$	0.74	0.11	0.03±0.12	0.74
Irrigation				
Whole Model	0.011*	$8.90_{3,200}$		
Rainfall	0.01*	6.37	-0.04±0.01	0.01*
Tsoil $\bar{x}$	0.80	0.05	0.02±0.08	0.81

CHAPTER 5

Conclusion

My dissertation has aimed to focus on how changing rainfall patterns in tropical and arid environments affect leaf litter frogs and lizards respectively, at different temporal and spatial scales. The current paradigm for addressing the impacts of climate change on frogs and lizards is focused on thermal niche shifts driven by increased global temperatures (Sinervo et al. 2010; Huey et al. 2012). To better assess the extinction risk of species and population from climate change it is important to investigate changes in the critical resource of water (Cahill et al. 2012). To date, the role of water availability as a critical resource, in terms of deluges or droughts, is in its infancy, but my dissertation provides evidence that entire communities, and individual species, show strong responses to changing rainfall patterns. These changes range from tropical frogs in wet environments having a negative response to too much rainfall, to daily lizard behaviors being determined by sporadic rainfall in an arid environment. These studies provide evidence that species responses to climate change are more complicated than simply changes in temperatures, because temperature and hydrologic cycles are changing concurrently. Understanding the role of both factors should allow for better forecasting of species responses, both negative and positive, to future climate change.

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