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

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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.

Key words: community; diversity; ENSO; leaf litter; rainfall; tropics.

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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 and data collection

LCBS protects ~300 ha 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 to 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

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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 × 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 to 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

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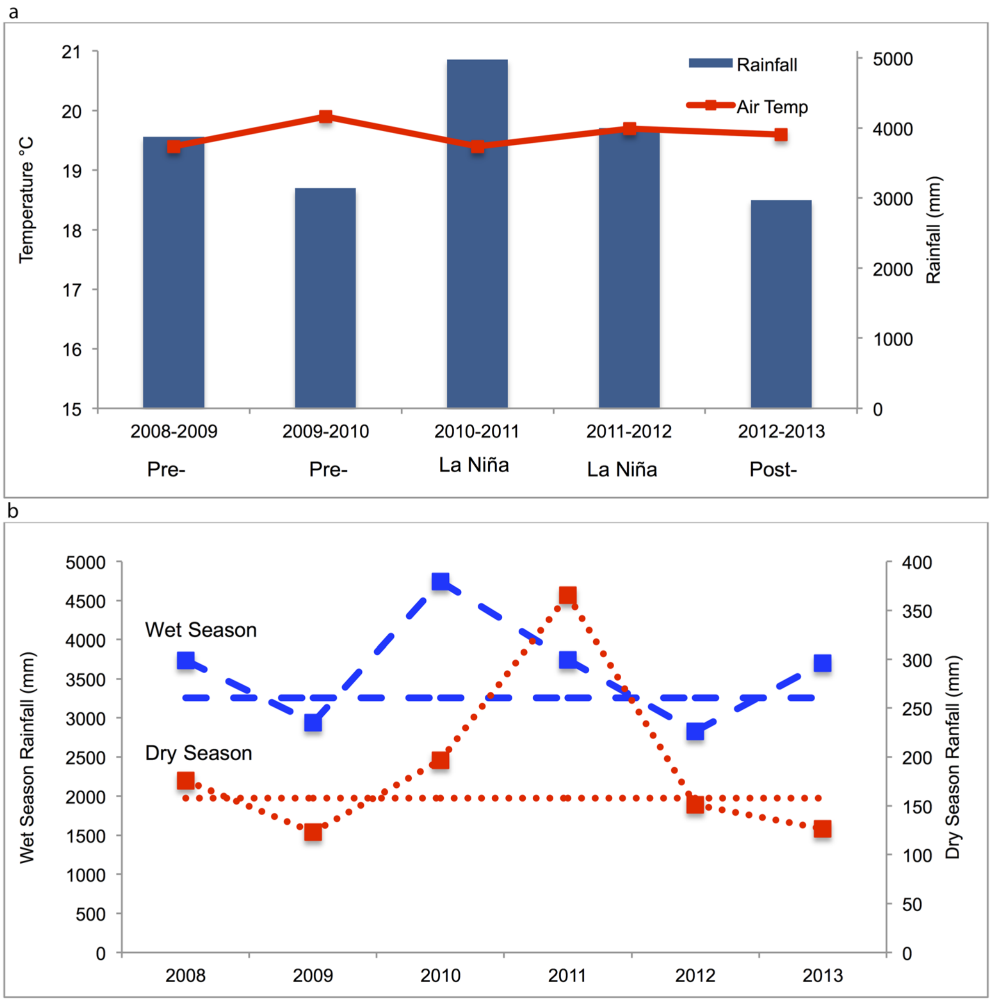

Fig. 1. (a) Mean annual temperatures and 12-month rainfall totals measured from March to February for each sampling year. This La Niña was strong from July 2010 to April 2011, followed by a 4-month lull, reemerging to slightly weaker La Niña conditions from September 2011 to March 2012 (Hu et al. 2014). (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.

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

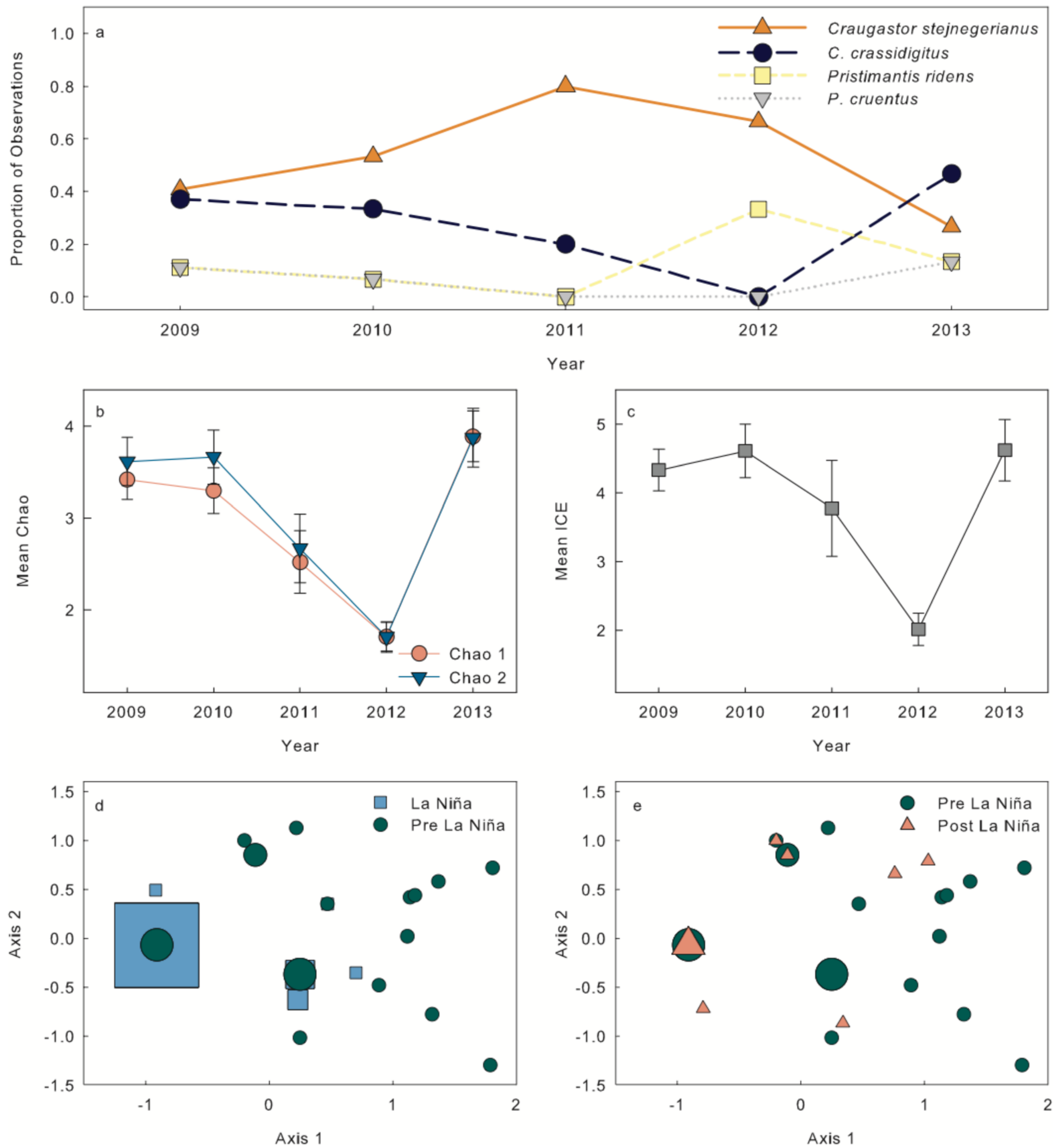

Fig. 2. Terrestrial frog community changes in response to La Niña. (a) Proportion of total frog observations for each species (orange triangle = *Craugastor stejnegerianus*; navy circle = *C. crassidigitus*; yellow square = *Pristimantis ridens*; grey inverted triangle = *P. cruentus*) through time. Species diversity index plots of (c) Chao1 (peach circle) and Chao 2 (blue triangle) and (d) ICE (grey square) 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 circle) versus La Niña (blue square). (e) NMDS ordination of pre-La Niña (green circle) versus post-La Niña (pink triangle) 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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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 × La Niña			
P	0.0004*	0.0003*	0.0140*
Z	−3.55	−3.56	−2.44
χ^2	12.73	12.83	6.03
La Niña × Post-La Niña			
P	0.0005*	0.0007*	0.0274*
Z	3.47	3.38	2.18
χ^2	12.25	11.59	4.86
Pre- × Post-La Niña			
P	0.012*	0.21	0.98
Z	2.49	1.02	0.00
χ^2	6.31	1.51	0.00

than during the La Niña for all species combined ($F_{1,38} = 8.66$; $P = 0.005$). Post-La Niña plot occupancy rebounded to pre-La Niña levels ($F_{1,28} = 1.91$; $P = 0.177$). 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).

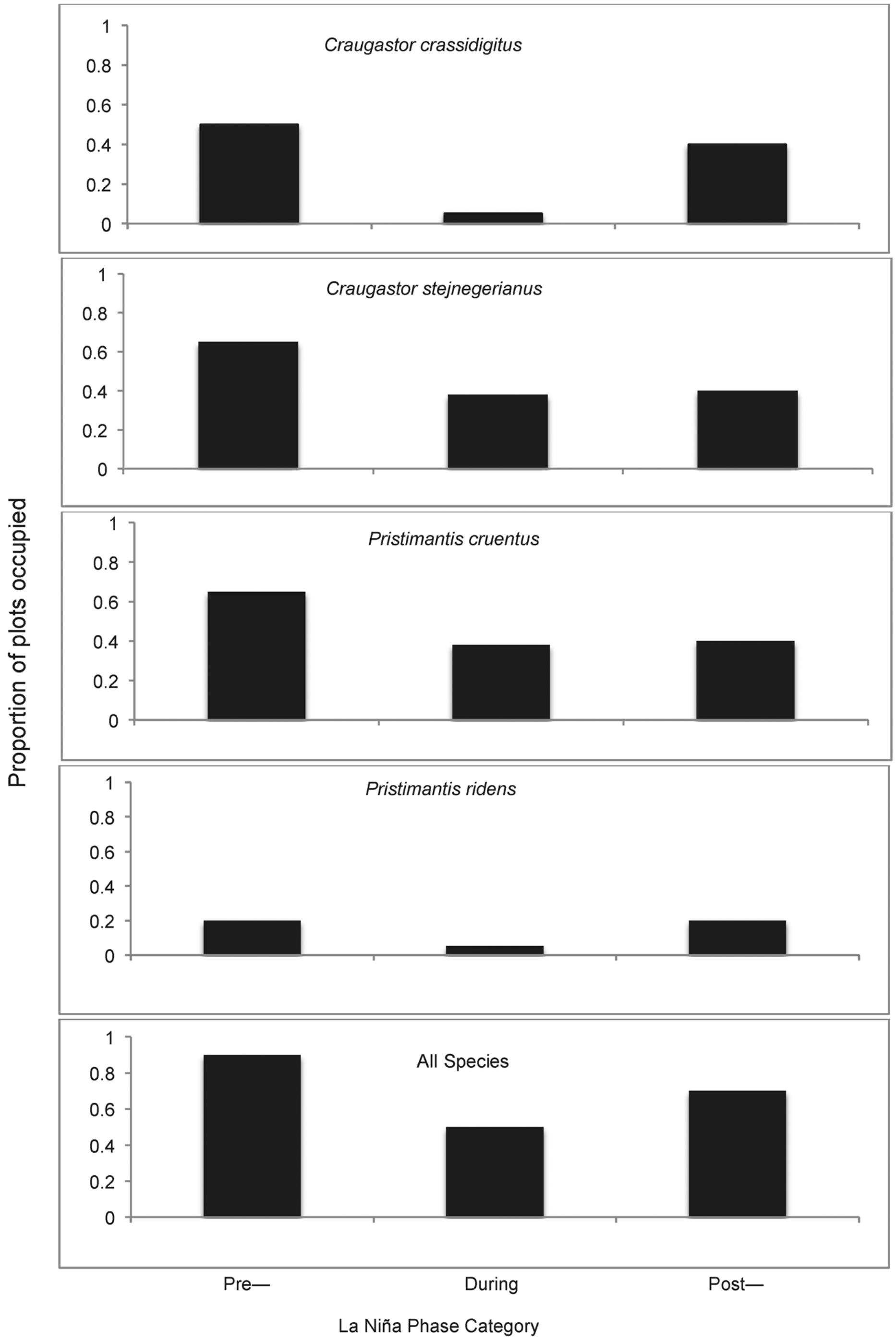

Fig. 3. Percentage of plots occupied by each species for the three La Niña phase categories.

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

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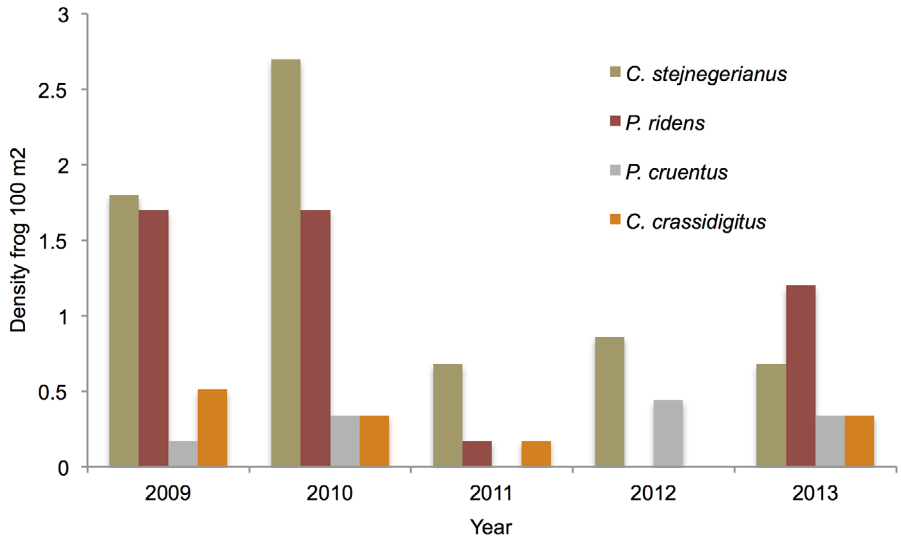

Fig. 4. Annual variation in frog densities as shown from leaf litter plot sampling periods 2009–2013.

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

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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.

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