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Assessing sensitivity to climate change and drought variability of a sand dune endemic lizard

Cameron W. Barrows [a,*], John T. Rotenberry [a,b], Michael F. Allen [a]

[a] Center for Conservation Biology, University of California Riverside, Riverside, CA 92521-0334, USA
[b] Department of Biology, University of California Riverside, Riverside, CA 92521-0334, USA

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ABSTRACT

Bioclimatic models aimed assessing a species' sensitivity to climate change incorporate mean shifts in climate variables; however the more acute threat to the persistence of species may result from increased frequency of extreme climatic events, including increased duration and severity of droughts. Here we assess climate-change sensitivity using niche modeling that unlike bioclimatic modeling incorporates both climate variables as well as other habitat features that constrain a species' distribution. We analyzed the effects of potential increases in drought frequency for an endangered, sand dune-restricted lizard, a species restricted to a narrowly occurring substrate and so unable to move up-slope or pole-ward to track climate shifts. Our niche modeling results indicated only minor losses to the area of suitable niche space at lower levels of modeled climate change; at the most severe climate shifts we tested the area of suitable niche space reduced by slightly more than 50%. However, extrapolating the potential impacts of reduced rainfall on drought periodicity and intensity showed a more immediate and acute impact on the lizard's populations. Drought duration projections coupled with landscape fragmentation resulted in rapid losses of suitable niche space, beginning in the more arid portion of the lizard's range and extending into more moderate climate areas. Although there is greater uncertainty associated with the impacts of climate change on drought periodicity than with shifts in mean conditions, our results show a greater potential for droughts to negatively impact species' resilience to such changes.

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1. Introduction

The climate change scenarios presented in the 2007 IPPC report (IPCC, 2007; Kerr, 2008), provide unique opportunities to evaluate the ecological impacts of modeled changes on organisms. Most predictions of climate change-related impacts focus on re-distribution, either up-slope and/or pole-ward as organisms track shifting climate envelopes (Araújo et al., 2004; Parmesan, 2006). Range contractions are expected where distributions are artificially isolated in reserves surrounded by altered landscapes (Araújo et al., 2006) or when other factors constrain the ability of species to follow shifting climatic envelopes. Recent climate-correlated extinctions of American picas, *Ochotona princeps* (Grayson, 2005), restricted to often isolated high elevation mountains, provides an empirical example of climate change's impacts on species with "no where to go." For species unable to traverse naturally isolated or more recently altered landscapes, a species' sensitivity to shifts in temperature and/or precipitation may be an important predictor of their ability to avoid extinction related to climate change.

In the absence of accurate local-scale predictions of abiotic changes (Root and Schneider, 2002), bioclimatic modeling can provide insights as to the sensitivity of species to a range of climate change scenarios (Preston et al., 2008). Although bioclimatic modeling has been criticized for over-simplifying what are inherently complex habitat relationships, such models may provide important insights into the biotic interactions as well as anthropogenic constraints that impact a species' sensitivity to climate change (Pearson and Dawson, 2003; Preston et al., 2008). Increasing variability is a fundamental part of climate model predictions, but there is greater uncertainty as to how it will be manifested and variation has not been explicitly incorporated in estimating impacts on species. In evaluating the sensitivity of species to climate change, climate variability may be as, or even more important than shifts in mean values as drivers of species responses (Parmesan et al., 2000; Morris et al., 2008). For species lacking the mobility to track the annual availability of resources at regional or larger scales, drought intensity and duration may be a greater driver of persistence rather than longer term shifts in mean precipitation.

Here we present results from both niche modeling and an analysis the effects of increases in drought frequency for assessing the climate-change sensitivity of the narrow endemic, sand

* Corresponding author. Tel.: +1 760 834 0594.
E-mail address: cbarrows@ucr.edu (C.W. Barrows).

dune-restricted Coachella Valley fringe-toed lizard, *Uma inornata*. We selected a niche modeling (Rotenberry et al., 2002, 2006; Browning et al., 2005) rather than a more constrained bioclimatic modeling approach as niche models explicitly incorporate variables characterizing other habitat features in addition to just climatic variables. Reptile and amphibian populations may be particularly sensitive to climate change due to their limited mobility (Root and Schneider, 2002; Hannah et al., 2005; D'Amen and Bombi, 2009). The federally (US) threatened *U. inornata* has been the focus of local conservation efforts in one of the driest, hottest portions of North America's Sonoran Desert (Barrows, 1996, 1997, 2006). It occurs in a region expected to experience among the largest temperature and precipitation shifts related to climate change within temperate North America (Kerr, 2008; Seager et al., 2007).

For *U. inornata*, with an edaphic-restricted range, fragmented habitat reserves surrounded by suburban development, and within a region expected to experience substantial climate shifts, the prognosis for long-term sustainability in a changing climate would seem dire. Research modeling the impact of a congener occurring in central Mexico, *U. exsul*, a species also restricted to an isolated sand dune system, predicted substantial loss of modeled habitat in response to climate change (Ballesteros-Barrera et al., 2007). For both species shifting their distribution up-slope or pole-ward is not an option. However, an alternative hypothesis considers the broad range of climatic conditions these lizards have evolved with. In extremely arid deserts variation in annual precipitation increases with decreases in mean annual rainfall (Noy-Meir, 1973; Bell, 1979; MacMahon, 1979). Having evolved in such a highly variable environment may afford some resilience to a changing climate.

The occurrence patterns of *U. inornata* are well understood; habitat occupancy is a function of the distribution and compaction of aeolian sand, while annual population dynamics are closely tied to patterns of sand accumulation and precipitation (Barrows, 2006). These straightforward habitat relationships have resulted in successful habitat and niche modeling efforts (Barrows, 2006; Barrows et al., 2008). Importantly, the lizards cease reproductive activities when annual precipitation drops below 50 mm, thus establishing a critical threshold for positive population growth (Barrows, 2006). Our initial approach here involved developing a niche model based on the lizards' historic and current distribution, then fitting that model onto a landscape of increasing summer temperature and reduced precipitation. The range of conditions for which we modeled the lizards' niche response followed those projected for the broader southwestern US, with reductions in mean annual precipitation from 35 to 75 mm and increases in mean summer temperatures of 1–2 °C (Seager et al., 2007; Hayhoe et al., 2004). With species-specific drought response data in hand, we then estimated how reduced precipitation could result in increased droughts and how the duration of those droughts could impact the sustainability of the lizard's populations across its range.

2. Methods

2.1. Study area and historic data sources

Our study area was confined to the Coachella Valley of Riverside County, California USA (Fig. 1). We collected historic data on lizard locations from a variety of sources including the University of California Museum of Vertebrate Zoology, California Academy of Sciences, and California Natural Diversity Data Base of the California Department of Fish and Game. Current location data was collected on permanent plots over the past 7 years (Barrows and Allen, 2007a). Additionally, biologists with a focused interest on this region's reptiles and 20 plus years of surveying in the Coachella Valley were interviewed. All museum locality records and biologists' sighting locations were georeferenced to <150 m resolution. The variety of sources meant that not all data were collected in a systematic or repeated manner; therefore, they document presence only. These sources yielded 110 spatially non-redundant locations (i.e., locations at least 150 m apart) for the fringe-toed lizard.

2.2. Niche modeling

For niche (bioclimatic) modeling we used the partitioned Mahalanobis distance statistic (D^2) (Clark et al., 1993; Knick and Roten-
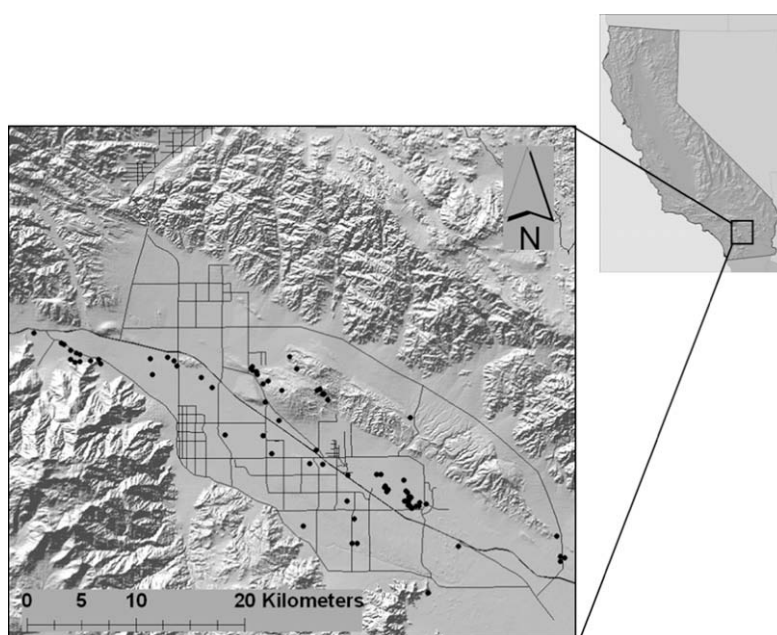

Fig. 1. Location map showing the position of the Coachella Valley within the state of California, USA. Major roads are depicted as black lines; Coachella Valley fringe-toed lizard locations used to calibrate the niche model are shown as black dots.

berry, 1998; Dunn and Duncan, 2000; Rotenberry et al., 2002, 2006; Browning et al., 2005) to model the current distribution of similar habitat. To distinguish between modeled habitat similarity versus measured habitat on the ground, we refer to the model output as "suitable niche space". The partitioned Mahalanobis statistic yields for any location an index of its similarity (habitat similarity index, or HSI; scaled 0–1) to the multivariate mean of environmental characteristics based on known locations of the target species. Each point on a map containing values for the environmental variables can be scored for its HSI, and these values plotted to generate the likely distribution of suitable niche space (e.g., Fig. 2). Variables used to model the potential distributions of the *U. inornata* included slope, mean maximum temperatures in July (MAXTJUL), mean annual precipitation (MPRECIP), four soil classifications quantified as the number of 30 × 30 m cells classified as soil map unit within a 150 × 150 m area: Myoma fine sand 5–15% slope, Myoma fine sand 0–5% slope, Carsitas gravely sand 0–9% slope, Carsitas cobbly sand 2–9% slope (Soil Conversion Service, 1980),

and a community defined by ephemeral surface sand availability (Barrows and Allen, 2007a) quantified as the number of 30 × 30 m cells classified as a community map unit within a 150 × 150 m area. We randomly selected 80 *U. inornata* occurrence records to include in the calibration dataset used to create the model. A remaining 30 records were used as validation records to evaluate model performance. The base map of environmental layers consisted of 75,687 150 × 150 m cells, encompassing an area of 170,296 ha.

Using the best performing niche model (model/partition with the highest median HSI values and that best predicted the validation data), we then recalculated each map point's estimated HSIs based on projected changes in its climate variables, MAXTJUL and MPRECIP. We changed climate variables incrementally, increasing MAXTJUL by 1 and then 2 °C, and decreasing MPRECIP by 35, 55, and 75 mm. Because temperature and precipitation vary together across the Coachella Valley, with cooler-wetter conditions in the west and hotter-drier conditions in the eastern portions of the valley, we shifted both variables in concert for all possible combinations. For each new model the area of suitable niche space (HSI values ⩾ 0.5) in ha was calculated and the distribution of that suitable niche space was mapped.

2.3. Drought estimations

Using mean annual precipitation data for the Coachella Valley (Western Regional Climate Center, Upper Snow Creek, Palm Springs, and Indio reporting stations), we calculated the occurrence and duration of regional droughts. Annual rainfall totals for each location were then incrementally reduced by 35, 55 and 75 mm, as was done for the bioclimatic/niche models, to determine the possible effect of such reductions drought durations. Our drought threshold was based on a nearly 20-year data set of population growth (λ) for *U. inornata*; positive λ values occurred only when annual precipitation exceeded 50 mm (Barrows, 2006). We used a mean value for annual survivorship derived from a 25 year mark-recapture study of *U. inornata* where annual mortality was about 50% regardless of annual variation in weather conditions, and few individuals lived more than 5 years (M. Fisher and A. Muth, pers. comm.). Coupling known values for mean survivorship, longevity and a threshold for positive population growth allowed us to estimate population sustainability in response to droughts extending multiple years; droughts ⩾5 years would result in population declines exceeding 95%, likely leaving too few adults to rebuild the population when wetter conditions resumed.

3. Results

3.1. Niche modeling

Using our niche model of current suitable niche space as a baseline, when mean precipitation was decreased by 35 mm and July temperatures were increased by 1 °C, there was a 2% decrease in suitable niche space (HSI ⩾ 0.5) compared to the current habitat extent. When mean precipitation was decreased by 55 mm and July temperatures increased by 2 °C, there was a 32% decrease in suitable niche space from current conditions; when mean precipitation was decreased by 75 mm and July temperatures increased by 2 °C, there was a 55% decrease in suitable niche space from the current habitat extent (Fig. 2).

3.2. Drought simulations

We then estimated the effects of multiple-year droughts, assuming the current level of variance in precipitation and then
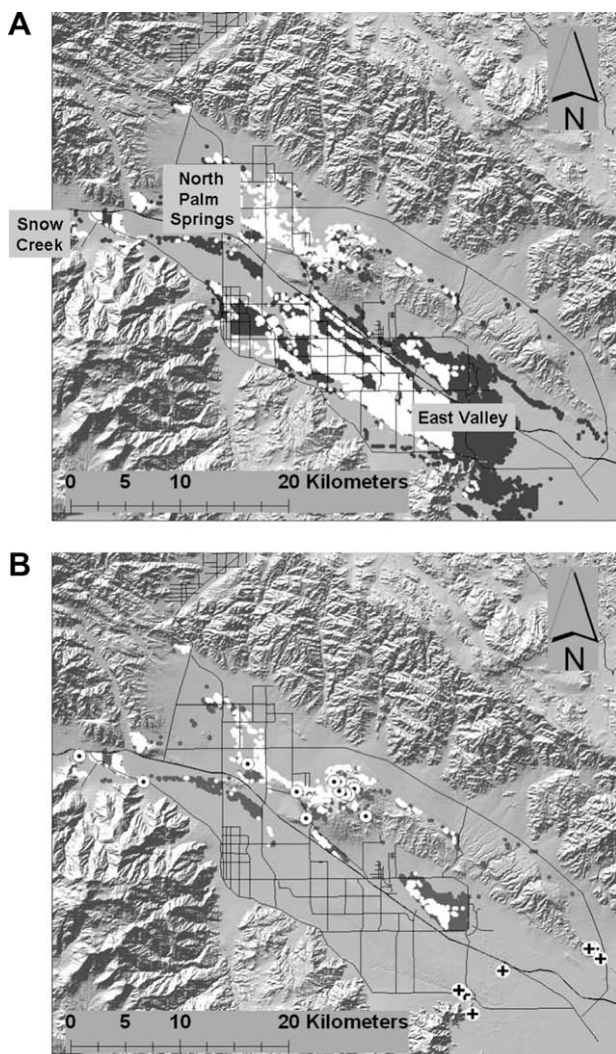

Fig. 2. Our Coachella Valley study area showing topographic features, major roads (black lines) and modeled suitable niche space for *Uma inornata*. "A" = historic conditions, "B" = current conditions with the habitat loss from existing development accounted for. Modeled suitable niche space areas were based on HSI values ⩾ 0.5; gray + white = current climate envelope, white alone = climate envelope with an increase of 2 °C mean July maximum and a decrease of 75 mm annual rainfall. White circles with black centers depict locations of isolated western habitat patches; black crosses within white circles depict locations of isolated western habitat patches.

reducing annual rainfall by the same amounts as we did with the bioclimatic models. Under current conditions, since 1928, there have been no droughts with annual rainfall ⩽ 50 mm that have exceeded three consecutive years anywhere within the range of *U. inornata* (Fig. 3). There was one five year sequence, from 1999 to 2003, when that sequence exceeded 50 mm only in 2001 (when it was 55 mm) for the east end of the valley. Within that drought year sequence, 2002 had the lowest rainfall on record (⩽4 mm fell on the eastern-most portions of the lizards' range).

When we reduced annual rainfall amounts by 35 mm, the drier eastern valley had multiple consecutive drought year sequences that were ⩾5 years in length (Fig. 3). Further west, near Palm Springs, with a 35 mm reduction there were no drought sequence that reached 5 years in length. Still further west near Snow Creek, no severe drought sequences were projected. Reducing the annual precipitation by 55 and then 75 mm resulted in increasing the number of ⩾4–6 year drought sequences from the eastern edge of *U. inornata's* range through Palm Springs, but still none occurred as far west as Snow Creek.

Empirical evidence for the population impact of consecutive year droughts on *U. inornata* was provided by the drought sequence from 1999 to 2003. Prior to the drought, each of the isolated habitat patches shown in Fig. 2B was occupied by *U. inornata*. Following that drought the eastern-most patches were no longer occupied whereas *U. inornata* still occurred on all of the western patches. There was no statistical difference in patch size between the eastern and western sites (occupied sites mean = 8.9 ha, $n = 12$; abandoned sites mean = 8.4 ha, $n = 7$; t-test, $p = 0.927$). Mean annual rainfall during that 5 year drought ranged from 25 to 31 mm at the eastern sites; on the western sites mean rainfall ranged from 56 to 173 mm.

4. Discussion

Using a niche modeling approach alone, our results lend support to a hypothesis that evolving under high levels of climate variation offers resilience to climate change (Huey et al., 2009); 45% of current suitable niche space persisted in the face of the most severe conditions we modeled. These lizards have shown an ability to sustain populations on relatively small habitat patches (Barrows and Allen, 2007b). Thus, based on our niche modeling results, we would predict that most *U. inornata* populations would likely avoid extinction at even the higher levels of modeled climate change for the region.

With no recruitment during drought years of annual rainfall ⩽ 50 mm (Barrows, 2006), and with a consistent annual mortality rate, we had the rare opportunity to assess species-specific impacts of droughts. For fringe-toed lizards five consecutive drought years would result in a population decline of 97%; for droughts of 6 years in duration the population decline would be >98%. Under those levels of population decline only large, unfragmented populations would likely avoid extinction. Our models indicate that the negative impacts on *Uma* populations of prolonged droughts precede those of niche model-based mean climate shifts in a wave of progressively severe climate change from east to west. In principle, those differences would be lessened across an unfragmented landscape. Stochastic droughts would likely reduce or even eliminate local populations to the east, but immigration from less impacted populations to the west could repopulate those sites when suitable rainfall conditions resumed, providing a mean ongoing level of occupancy. Western populations would serve as population sources whereas populations further east would be long-term population sinks. With increasingly dry conditions and increased drought frequency the threshold between population
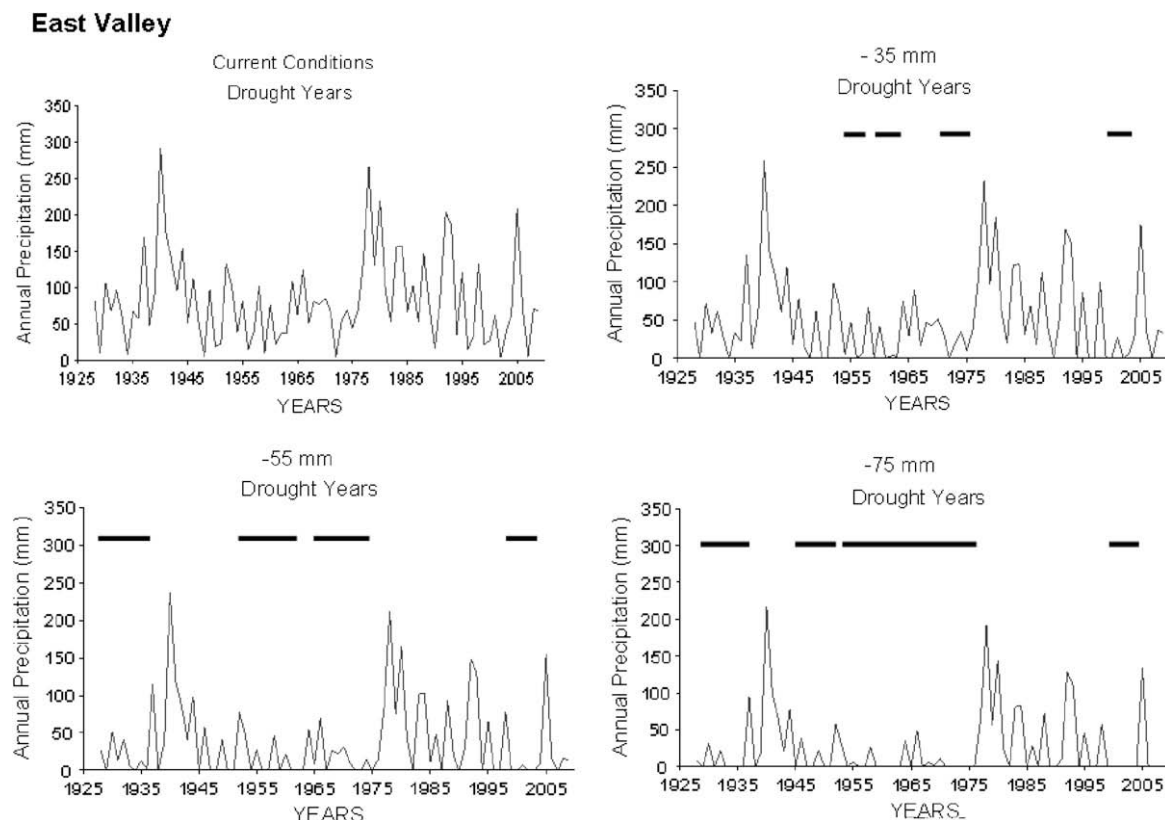

Fig. 3. Current and extrapolated drought periodicity and duration, based on droughts defined as ⩽50 mm precipitation (Barrows, 2006), at three locations spanning the rainfall gradient of the Coachella Valley. Horizontal bars indicate droughts of ⩽50 mm of annual rainfall and ⩾5 years in duration. Locations are shown in Fig. 2A.
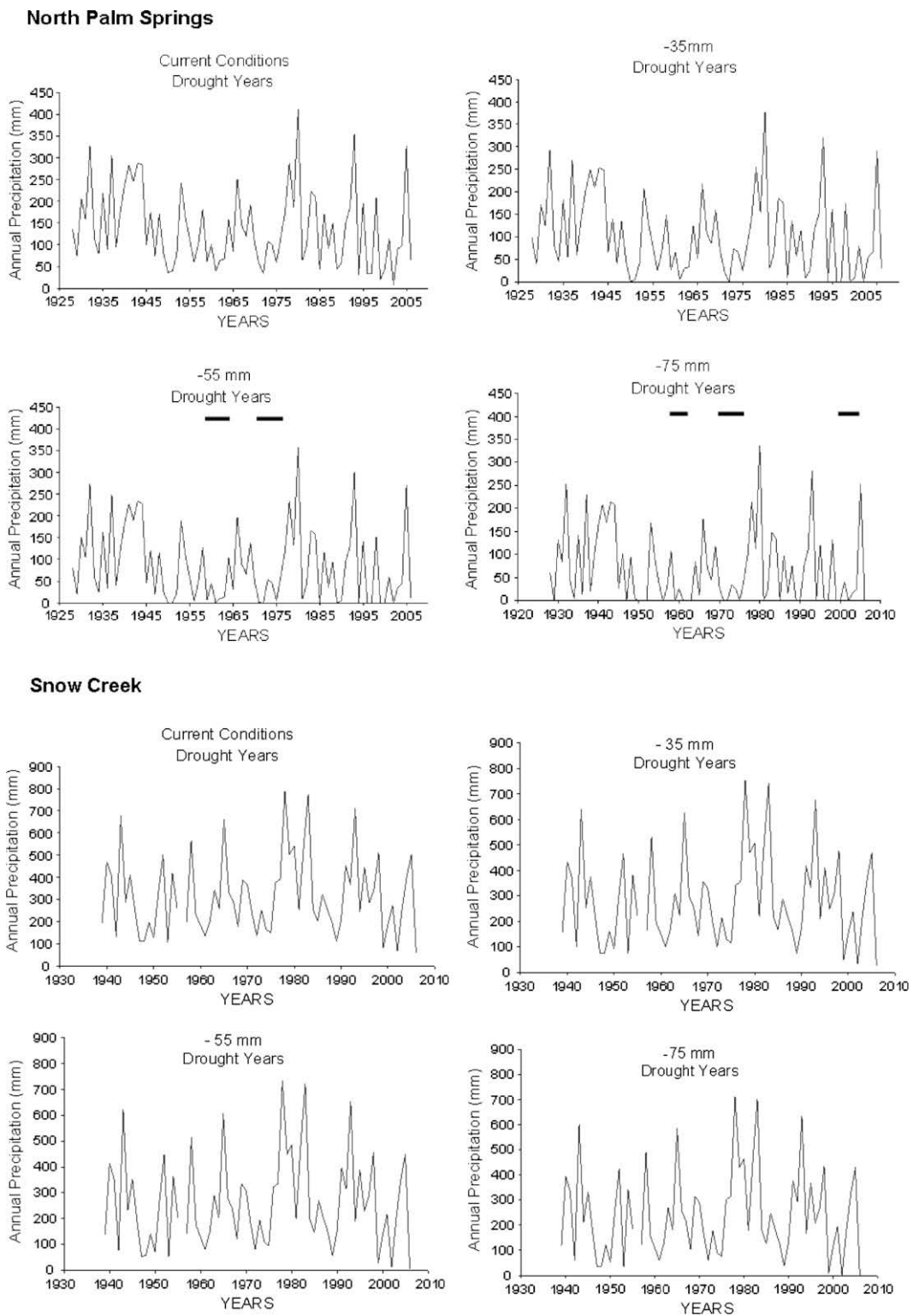
North Palm Springs

Snow Creek

Fig. 3 (*continued*)

sources and sinks would shift westward. The amount and distribution of structurally suitable sand dune habitat remaining unoccupied by *U. inornata* would be a function of the frequency of prolonged droughts, distance to source populations, and the lizards' immigration rates.

The fringe-toed lizard's narrow distribution, restriction to the aeolian sands, and 95% habitat loss (Barrows, 1996; Barrows

et al., 2008), are characteristics of a species with a high level of vulnerability to climate change (Root and Schneider, 2002). The Coachella Valley is a highly fragmented landscape with little or no opportunity to repopulate areas once a prolonged drought's effect occurs. That prediction was empirically supported with the extirpation of several small, isolated fringe-toed lizard populations after the 2000–2004 drought years. As often is the case, fragmen-

tation in the Coachella Valley preceded the onset of conservation planning; however by including protected habitat reserves across the existing precipitation gradient, some of those populations appear resistant to even the most extreme predicted effects of climate change. While modeled *U. inornata* distributions were resistant to mean climate shifts, our results support a hypothesis that that increased drought frequency may have a more immediate and acute impact on populations than shifts in mean climate (Parmesan et al., 2000; Morris et al., 2008).

Narrowly distributed habitat specialists may be especially vulnerable to the negative impacts of climate change (Root and Schneider, 2002; Ballesteros-Barrera et al., 2007). These same species are often the focus of conservation planning efforts; the negative synergy of climate change along with other stressors such as fragmentation must be a key consideration in conservation designs (Hannah et al., 2005). Climate change can increase levels of fragmentation (Kourmoundouros et al., 2009) and fragmentation can exacerbate climate change effects when it results in barriers preventing species from tracking shifting preferred climate envelopes (Araújo et al., 2004). Our analysis here demonstrates a mechanistic approach, tying climate sensitivity to demographic responses to climate and fragmentation patterns for assessing the impacts of climate change for a narrow endemic species. Although our results are specific to a single species, they indicate that bioclimatic models that incorporate only incremental shifts in mean temperature and precipitation could grossly underestimate the true impacts of climate change on world-wide biodiversity.

Acknowledgements

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