Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Title Page

Title:

Analysis of climate paths reveals potential limitations on species range shifts

Running title:

Climate paths

Author affiliation:

Regan Early (corresponding author): Cátedra Rui Nabeiro - Biodiversidade, Universidade de Évora.
Casa Cordovil 2ª Andar, Rua Dr. Joaquim Henrique da Fonseca, 7000-890 Évora, Portugal
Email: regan.early@gmail.com
Telephone: (+351) 266 759350
Fax: (+351) 266 759373

Dov F. Sax: Department of Ecology and Evolutionary Biology, Brown University, Box G-W, 80 Waterman Street, Providence, RI, 02912, USA
Email: dov.sax@gmail.com

Type of article: Letter

Authorship statement: RE and DS devised analytical approach, RE performed analyses, RE and DS wrote manuscript.

Word count:
Abstract – 150
Main text – 5030
Figures – 4
Tables – 2
References – 50

Keywords:

Landscape ecology, dispersal, population persistence, climate variability, fundamental and realised niche, salamander, anura, assisted migration, translocation.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Abstract.

Forecasts of species endangerment under climate change usually ignore the processes by which species ranges shift. By analysing the ‘climate paths’ that range shifts might follow, and two key range-shift processes - dispersal and population persistence - we show that short-term climatic and population characteristics have dramatic effects on range-shift forecasts. By employing this approach with 15 amphibian species in the western USA, we make unexpected predictions. First, inter-decadal variability in climate change can prevent range shifts by causing gaps in climate paths, even in the absence of geographic barriers. Second, the hitherto unappreciated trait of persistence during unfavourable climatic conditions is critical to species range shifts. Third, climatic fluctuations and low persistence could lead to endangerment even if the future potential range size is large. These considerations may render habitat corridors ineffectual for some species, and conservationists may need to consider managed relocation and augmentation of *in situ* populations.

Introduction:

Climate change has contributed to pronounced changes in the geographic distribution of species over the past several decades (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006). Over the remainder of this century, climate change is expected to cause many more species’ ranges to shift, collapse or expand - leading to a major reorganization of ecological communities and biodiversity loss (Walther 2010). The predominant approach for forecasting species’ range-responses to climate change

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

uses climate at the locations a species currently occupies to evaluate the temperature and precipitation conditions that permit a positive net population growth rate, i.e., bioclimatic niche modelling (Soberon 2007). These bioclimate models are then used to predict the geographic locations that the species could potentially occupy at some point in the future, and risk assessments are based on assumptions about the species' ability to shift its range to these locations. For example, it may be assumed that a species cannot disperse beyond its current range or alternatively that it can disperse to any place that will be climatically suitable for it (e.g. Thuiller *et al.* 2005). These assumptions can be used to estimate the extremes of extinction likelihoods, but provide no insight into the actual range dynamics that will play-out during range shifts.

Here we map the 'climate paths' along which species' ranges may shift, i.e. the paths formed by the location of places with suitable climatic conditions during a sequence of time steps. We use measures of dispersal and population persistence to predict range dynamics along these paths. Most previous analyses of this kind have assumed an evenly graduated change in climate, which would facilitate gradual and steady range shifts (Brooker *et al.* 2007; Anderson *et al.* 2009). In reality, climate change is likely to be highly dynamic, with short-term fluctuations both above and below a directional trend (Easterling *et al.* 2000; Wang & Schimel 2003). This may cause species to colonise new areas during episodic warm periods, and to pause or temporarily retreat during cool periods (Walther *et al.* 2002; Jackson *et al.* 2009). In such an environmental regime, range expansions would be aided if populations could survive short periods when climate is unfavourable for them. This would prevent ranges from contracting during cool episodes. Then, when conditions improve, populations that survived at a range margin would produce dispersing individuals that could further extend the species' range (Jackson *et al.* 2009). Range expansion rates would also increase with the distance that individuals could disperse in a given time step (Anderson *et al.* 2009). Range-shift predictions have only recently begun to consider dispersal (Williams *et al.* 2005; Anderson *et al.* 2009; Engler & Guisan 2009), and to our knowledge persistence and climate variability have yet to be considered explicitly. We investigate the importance of these processes using 15 amphibian species endemic to the western USA, for the time period between 1990 and 2100.

Limited empirical data on population processes often restrict the scope of range-dynamic forecasts to a few, well studied species (Anderson *et al.* 2009; Engler & Guisan 2009). We circumvent this limitation by 'experimenting' with different values for species' traits. This yields principles regarding the relative importance of persistence and dispersal, given the different ways in which climate paths might advance, that are widely applicable outside this study system.

Material and Methods:

Species distribution data - We conducted analyses for amphibian species whose entire range lies west of the 100th meridian – amphibian ranges rarely cross this meridian, which divides the Rocky mountains and Great Plains from the east of the USA. Of these species we used only those whose ranges fall entirely within USA borders and for which sufficient bioclimate modelling data were available (15 species). Species point occurrences from 1961-90 were taken from Global Biodiversity Information Facility (http://www.gbif.org). Occurrences that could not be confidently geo-referenced were discarded. We used the most current phylogeographic studies to assign location records to the correct species (S1). Species range polygons were taken from the IUCN Red List website (IUCN 2008).

Climate variables - Bioclimate models were built using means from 1961-90 of the following variables: mean annual temperature, mean temperature of the coldest month, mean temperature of the hottest month, mean annual precipitation, mean monthly winter precipitation (January to March) and mean monthly summer precipitation (June to August). These variables reflect critical periods in the life history of west coast amphibians. Winter precipitation and temperature govern snowfall, snowmelt and hydroperiod, which in turn affect success of aquatic reproduction and terrestrial breeding behaviour (Blaustein *et al.* 2001; Corn 2003; McMenamin *et al.* 2008). Summer precipitation and temperature are linked to larval and adult mortality (Corn 2005). Range shifts were projected using predictions from the Hadley CM3 (HCM) and PCM3 (PCM) General Circulation Models (GCMs) throughout the period 1991-2100, using A2 and B1 emissions scenarios. Climate predictions that were bias-corrected and spatially downscaled (to 1/8º, approximately

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

140 km^2, resolution) as described by Maurer et al (2007) were taken from http://gdo-dcp.ucllnl.org/downscaled_cmip3_projections/.

Bioclimate modelling - For our focal species, we evaluated the utility of four bioclimate modelling techniques: Generalized additive model (GAM), Mahalanobis distances, Bioclim and Maxent (S1). Of these approaches, GAMs minimized false presences and absences creating the most reliable models for most species (S1) and we thus base our results on a GAM approach. We used species occurrence points to construct GAMs using thin plate regression splines and Generalised Cross Validation (GCV). We multiplied the degrees of freedom in the GCV score by 1.4 to create smoother models, in light of the small number of species occurrences (Table 1). Since no absence data were available, we randomly sampled pseudo-absences (twice as many as the number of presences for each species) from the 1500 cells (~210000 km^2, a region with radius ~ 150km) surrounding the cells a species occurred in. See S1 for further details on the choice of sample region. Cells classed as pseudo-absences could in fact be climatically suitable. This, combined with the small number of records, reduced our confidence in an individual model’s ability to accurately discriminate between suitable and unsuitable climatic conditions. Therefore, we repeated the pseudo-absence sampling process to build 100 bioclimate models for each species. If one of the 100 GAM algorithms could not converge on a single model it was discarded and a new set of pseudo-absences were sampled. The consistency (correlation) between these models reflects the degree to which each species’ climate niche is genuinely distinct from the surrounding environment. For

1961-90 and decadal future climates, we calculated the mean suitability predicted for each grid cell by all 100 models, to produce a composite suitability map.

We classified cells as suitable or unsuitable according to a species-specific threshold that minimised the difference between sensitivity and specificity within the sample region. This approach weights omission and commission errors equally and is amongst the most accurate of thresholding techniques (Jiménez-Valverde & Lobo 2007). In a few cases we manually altered thresholds (S1). Model performance was assessed using deviance explained, AUC and false positive and false negative rates. The number of false positives was calculated in two ways. First we summed the number of grid cells west of the 100th meridian that were predicted to be suitable but which were not occupied. The false positive rate was calculated using the number of point occurrences for each species as the denominator rather than the number of absences, so as to demonstrate the degree of over-prediction relative to current range size. This false positive rate might be high even for accurate models, because under-recording can mistakenly lead to the appearance of false positives and because suitable climate space may exist too far from a species' range to be occupied. Thus, secondly we calculated the number of grid cells that were predicted to be suitable but which fell outside the expert-defined range polygons (IUCN 2008) and were 'seeded' using the criteria listed below. False positive rates were calculated for these data using the number of grid cells in the species range polygon as the denominator. Statistical analyses were conducted in R 2.9.2 (R Development Core Team 2009) incorporating the ROCR and mgcv packages.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Climate-path modelling - To construct climate paths we predicted the 1/8º grid cells predicted to be suitable for each species during each decade between the years 1991 and 2100 (‘climate space’). Decadal climate values were taken from the emissions scenario, averaged across the decade. We then simulated species progress along these climate paths each decade by implementing rules governing dispersal and persistence, as described in Table 2. Simulations were begun (‘seeded’) using all grid cells predicted suitable in 1961-90, excluding grid cells that were geographically disjunct from the species observed range (point occurrences and polygon) by more than six grid cells, or that were less geographically disjunct but were occupied by a congener known to competitively exclude the focal species. Thus, although areas distant from a species’ current range might be predicted to be suitable, they would not influence the starting point of climate path simulations.

Predicting IUCN status – For comparability, current and projected future IUCN statuses were calculated using the ‘Extent of Occurrence’ (EOO) criteria alone (Critically Endangered: < 100km^2, Endangered: < 5000 km^2, Vulnerable <20000km^2). Current EOO was calculated as the sum of the area of the cells that were climatically suitable between 1961-90. Statuses calculated from current EOO differed from IUCN statuses only if the IUCN status also considered population decline and habitat quality. Future EOOs were calculated as the mean area of the cells that were predicted to be occupied in the decades 2071-2099.

Results

Our analysis of climate paths revealed three key observations relevant to range dynamics under climate change.

1. Gaps in the climate path.

Given likely dispersal and persistence parameters, fluctuations around the directional trend of climate change can create gaps in climate paths. These gaps can prevent species from reaching climatically suitable regions, even in the absence of physical barriers to dispersal. Physical features, such as mountain ranges or desert regions can form barriers to range shifts because they contain areas that will not become climatically suitable for a given species over the time-scale of interest (Engler & Guisan 2009). However, gaps arise if some critical portion of a climate path is only available at a time step in which a species is unable to pass through it. For example, *Aneides flavipunctatus* may be unable to shift into its full potential future range because climate variability after 2050 causes the landscape connecting northern California and southern Oregon to become climatically suitable only transiently. This leaves insufficient time for the species to pass through the area (Fig. 1). Assuming different parameters made almost no difference to this outcome (Fig. 2). Graphs of the potential and occupied range size reveal the instances in which climatic fluctuations prevent progress along the climate path (S2). All species we examined showed at least some evidence that they will be unable to fully occupy the entire climate space projected to be available to them by 2100 because of a combination of permanent climatic barriers and temporary gaps in the climate path (Fig. 2, S2&4). Indeed, most species (11 of 15) are projected to occupy less than half of their available climate space by 2100 under at least some of the examined climate change and population parameter values (Fig. 4, S2 & 4).

2. Effects of dispersal and persistence on species' range-shift capacity

The ability to persist during short periods of unfavourable climate can be as important as dispersal ability in determining whether species can shift their range along a climate path and avoid range collapse. For example, the range-shift distance and range size of *Taricha torosa* in 2100 is more strongly increased by persistence during a single decade of unfavourable climate than it is by our high dispersal parameter (in which colonisation could occur across 24km/decade) (Fig. 3). This is the case for many other species (Fig. 2, S2-4).

The relative importance of dispersal and persistence depends on the dynamics of the climate path. For example, the climate path of *Batrachoseps nigriventris* advances fairly steadily (S3). High dispersal allows *B. nigriventris* to shift northwards every decade, regardless of its persistence ability (Fig. 4a-c). However, if the climate path advances jerkily, often retreating, the relative importance of dispersal and persistence is flipped. For example, dispersal ability affects *Rana draytonii*'s progress along the climate path very little, but the ability to persist in place through one decade of unfavourable climate makes the difference between range collapse and range shift (Fig. 4d-f, S3). Both dispersal and persistence also affect outcomes for species whose

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

ranges do not shift along a climate path but remain in place or collapse. For example, the climate space of *Batrachoseps luciae* does not shift, but shrinks by 2100. *B. luciae* continues to occupy a wider proportion of its potential range throughout the 21st century given high dispersal and short-term persistence than without short-term persistence (Fig. 4g-i).

3. Future endangerment is not necessarily commensurate with species' future potential range size

Although none of the species examined are currently classed as Endangered or Critically Endangered, some species are likely to become endangered because their suitable climate space is projected to decrease (Fig. 2). However, we predict that many species will become endangered even though they are projected to have large areas of suitable climate space in 2100 (Fig. 2). These species decline because they are unable to shift into their future potential range due to gaps in the climate path caused by climatic fluctuation. These declines occur irrespective of the climate forecasts used, although there is variation in the precise number and identity of species in each risk category (S4). Species' available climate space is smaller on average under HCM (the General Circulation Model that indicates the greatest temperature increase) than PCM. For example, one species loses all climate space under PCM (A2 and B1), whilst three or four species lose all climate space under HCM (A2 and B1 respectively, Fig. 2, S4). However, under low dispersal and no persistence three species become Critically Endangered under PCM A2 and B1, despite there being sufficient available climate space for them to remain Endangered or Least Concern. Under HCM A2 and B1 zero and two species respectively become Critically Endangered. Evidence that it is climatic fluctuation which limits range shifts in PCM climate forecasts comes from the effect of persistence. Allowing species to persist during periods of unfavourable climate had a significantly greater effect on the proportion of climate space that becomes occupied under PCM than under HCM (given low dispersal: paired t test, p=0.040 and p=0.015 for one or two decades persistence respectively), whereas the effect of increasing dispersal was not significantly different between HCM and PCM.

Discussion

Climate path analyses find that range shifts, expansions and contractions can be greatly affected by climatic variability, causing persistence to have a strong effect on whether species shift their ranges, and having unexpected and important implications for conservation plans. Climate paths evaluate the routes along which species ranges might move by dividing range shifts into time steps. The time steps used (decades in our analyses) reflect both the length of time over which the focal species could disperse and establish new populations, and the periodicity of the natural climatic oscillations within the study region. Climate forecasts cannot capture the spatial and temporal pattern of climate change with sufficient accuracy to predict the exact timing or location of range shifts. Instead, the purpose of the approach we suggest is to investigate how the spatio-temporal pattern of climate change places extrinsic limitations on species’ ability to shift their ranges. This gives us insight into how species' intrinsic traits might interact with the pattern of climate change to drive range dynamics. Below we discuss how the processes we investigate interact with each other and with other range-shift limitations.

Intrinsic traits that determine species' shifts along the climate path:

Recent research has found that dispersal ability can affect range-shift potential (e.g. Anderson *et al.* 2009; Engler & Guisan 2009), but to our knowledge this is the first time that the importance of persistence under short-term unfavourable climate conditions has been quantified. The degree of persistence that is required to prevent an advancing range margin from retreating when climate is poor depends on the degree and periodicity of climate variability. In our system, persistence for a single decade often had a strong effect because climatic fluctuations were strongly decadal (fig. 2, S4, Wang & Schimel 2003). Increasing persistence for a further decade tended to have a smaller effect, since periods of unfavourable conditions rarely existed in two contiguous decades. An important exception was *Taricha sierrae* under PCM A2, which did not survive at all given one decade persistence, but which remained 'Vulnerable' given two decades persistence regardless of dispersal ability (S4). The other notable exception was *T. torosa* under HCM B1 whose future range size given low dispersal was more than doubled by two decades persistence, producing almost the same result as high dispersal and two decades persistence (Fig. 3).

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Persistence will be determined by species' population demography, physiology and behaviour (e.g. occupying ameliorative microclimates) (Coulson *et al.* 2001; Green 2003; Reading 2007). For these amphibians we believe that persistence outside of their climatic tolerances for more than two decades is unlikely. Their longevity is not well understood but most appear to be reproductively active for less than a decade, and in addition to climate change their populations are threatened by non-climatic environmental stressors including habitat destruction, agricultural pollution, pathogens and invasive species (Hayes & Jennings 1986; Kiesecker *et al.* 2001; Davidson *et al.* 2002). The importance of the interaction between climatic variability, dispersal and persistence has been recognised theoretically (Jackson *et al.* 2009) but rarely examined in practice. Given the importance of persistence in driving range dynamics within this study and the global predictions of variability in the rate of climate change (Easterling *et al.* 2000; Wang & Schimel 2003), we recommend that collecting data on these traits should be an urgent priority.

Despite our emphasis on persistence, dispersal remains important for range-shifts. Dispersal ability is most important when the climate path moves steadily (*B. nigriventris*, Fig. 4a-c), and can interact strongly with persistence when the climate-path steps are large and uneven (*T. torosa*, Fig. 3). For the species we considered, our high dispersal parameter of 24km/decade is probably overly-optimistic. The majority of the species we studied are highly philopatric salamanders and newts, which have been recorded at a maximum of a few hundred metres from their home site (Smith & Green 2005). The other species are anurans, which can travel multiple kilometres, but are rarely expected to achieve 24km of dispersal in a single decade (Smith & Green 2005). For both groups, these dispersal distances are based on seasonal breeding migrations and there is no evidence this behaviour would facilitate migrations to new breeding areas. If maximum dispersal distances per decade are less than 12 km/decade (our low dispersal parameter), which is not unlikely for some species, then range collapse and extinction should be more common then we predict. Low average rates of dispersal may be bolstered by rare long-distance dispersal events (Engler & Guisan 2009). This would likely improve many of our species' range-shift abilities, given the gaps that appeared in their climate paths (Figs. 1 & 3). However, even less information is available with which to parameterise such occurrences than for average dispersal. We recommend that the triggers leading to dispersal and breeding outside the natal range, as well as the length of these dispersal events, become research priorities - as only this type of dispersal will drive range shifts.

Unanticipated consequences of climate forecasting technique:

We used two General Circulation Models, both thought to accurately represent climatic patterns across most of the study region (PCM and HCM3, Cayan *et al.* 2008), in order to bracket the range of possible outcomes. PCM is least sensitive to greenhouse gas forcing and shows the least overall climate change (Hayhoe *et al.* 2004). Thus, species' climate niches tend to move shorter geographic distances under PCM than under HCM (S3). However, the PCM model still predicts considerable fluctuations in precipitation in the study region. In fact, under some combinations of modelled conditions, PCM can even result in more Endangered and Critically Endangered species than HCM as climatic fluctuations make it harder for species to shift or maintain their range (Fig. 2, S4). Therefore it is not solely the directional magnitude of predicted climate change that is important; an increase in climatic variability could cause range collapse and inhibit range shifts.

An important note is that the climate change data used here are the average of multiple climate change simulations, and so are somewhat smoothed. Thus, in reality climate change may be even more variable, and persistence even more important than our estimates suggest.

The two greenhouse gas emission scenarios we used represent conservative (B1) and extreme (A2) estimates (Hayhoe *et al.* 2004). We have largely discussed examples using the B1 scenario in order to demonstrate that our findings are not simply caused by extreme climate predictions. Interestingly, outcomes under the A2 scenario are not always worse than under B1. For example, for *Taricha torosa* the higher degree of warming predicted under A2 created more future climate space than under B1 (S2). If *T. torosa* could reach this climate space then A2 might be less deleterious than B1.

Interaction of climatic and non-climatic restrictions on the climate path:

Both the presence of negative and absence of positive biotic interactions limit species current ranges and are likely to reduce the area and continuity of the climate

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

path (Araújo & Luoto 2007; Wiens *et al.* 2009). Consider, for example, what would happen if the climate paths of two competitor species coincide. Even if these species can co-exist at the landscape scale, at fine scales the presence of a competitor species will likely impede the establishment and the eventual size and number of populations of one or both species. Small, scarce populations produce few dispersing individuals and are poorly able to persist during unfavourable climates. Hence we expect that competition at fine scales would amplify gaps in species' climate paths. Such a situation is possible for at least one species in our analysis: *T. torosa*'s climate path takes it into the Sierra Nevada Mountains of eastern California (Fig. 2) where the closely related species *T. sierrae* is incumbent (Kuchta 2007).

The broad resolution of our analyses ensured that our predictions were based on general climatic trends, rather than local climatic predictions that are too specific to be realistic. However, at fine scales, species' vegetation, hydrology and microclimate requirements will likely limit the area and continuity of the climate path. In particular, anthropogenic landscape modification could form significant range-shift barriers. For example, *T. torosa* may need to cross the northern portion of the agriculturally intensive Central Valley (Fig. 3). This fragmented landscape will not only pose dispersal barriers but will reduce population size and thus persistence. Thus by restricting both dispersal and persistence, habitat fragmentation may be even more deleterious to range shifts than previously recognised.

Bioclimate models:

Calculating a species' climatic niche by correlating its locations with underlying climate data is subject to serious criticisms. One criticism is that these models assume that the species' distribution is in equilibrium with its environment and is not prevented from filling its entire niche, for example by dispersal limitations or biotic interactions (Soberon 2007; Wiens *et al.* 2009). While we cannot rule out the importance of this criticism in full, we have several reasons to believe that this criticism is of limited importance for the species we modeled. First, the composite GAMs we constructed seem well supported by the finding that the climate niches predicted were closely tied to distinct climate zones in California; for example the 'Hot Mediterranean' climate zone in western Sierra Nevada for *T. sierrae* and 'Hot Steppe' grassland for *Batrachoseps gregarious* (climate classifications from Russell 1926). Second, the models generally explained large quantities of deviance, had low omission rates and the area they predicted to be suitable coincided well with the expert-defined range (Table 1, S1). However, *Dicamptodon tenebrosus and Rana boylii* had high apparent omission rates. These rates are due to isolated populations and competitive interactions that exclude species from part of their climatically suitable range; nevertheless, these species' bioclimate models actually performed rather well (for further explanation see S1). Third, there was a good degree of overlap between multiple GAMs (S1). This suggests that species we studied genuinely occupy specific climate niches that are unique within the surrounding landscape. Finally, whilst performing more 'accurately' than the other approaches tested, composite GAMs predicted similar amounts of range loss and climate path variability to these approaches (S1). Thus our climate path results are unlikely to be artifacts of the modelling technique.

A second criticism is that bioclimate models assume that species cannot live under combinations of climatic variables that are different from those they currently occupy, i.e. ‘no-analog climates’ (Williams & Jackson 2007). It has been suggested that during the Pleistocene some North American amphibian species occupied climatic conditions that were not analogous to the species’ current range (Waltari *et al.* 2007). However, the refugia in which this occurred were in areas that were cooler and wetter than species’ current climate niches (Waltari *et al.* 2007). Precipitation is particularly important to amphibian distributions (Aragón *et al.* 2009), with effects on seasonal breeding habitat and food sources (Corn 2003, 2005). Precipitation change is predicted to change the hydrology of the study region substantially (Cayan *et al.* 2008). Therefore, persistence of the study species for long periods in the future under hotter, drier conditions than they currently experience seems more unlikely than in previous cooler, wetter conditions.

A third criticism is that species may adapt to changing climatic conditions, allowing them to survive in place (Wiens *et al.* 2009). This seems unlikely to be the case for our study organisms as a considerable amount of research has found little change in amphibian climatic niches over long periods of climate change (e.g. Kozak & Wiens 2006; Waltari *et al.* 2007; Vieites *et al.* 2009). Amphibian range shifts driven by

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Pleistocene climate change are common globally and within the study region (Green *et al.* 1996, Carstens *et al.* 2004; Steele & Storfer 2006; Araújo *et al.* 2008).

Regardless of these arguments, the ability of bioclimate models to predict into new time periods can rarely be tested. Consequently, we do not suggest that the species-specific predictions made here will be accurate, but instead that these models are sufficiently robust to demonstrate the likely scope of the species' range-dynamic responses to climate change.

Implications for Conservation Management:

We discuss three key management implications of our findings. First, constraints imposed by climatic variability, limited dispersal and low persistence may mean that even habitat corridors through high-quality habitat may not in themselves make range shifts possible. Additionally, corridors for species that show high uncertainty between climate paths under different GCMs are less likely to be effective. Where corridors are appropriate, their effectiveness will depend on how well the corridor landscape facilitates population persistence in addition to dispersal. Species' range shifts along corridors could be expedited by assisting or augmenting populations that 'naturally' establish themselves along the corridor. Given current uncertainty in climate modelling, predictions of climate paths many decades into the future may be an inadequate basis for corridor planning. However, the predicted directionality of range shifts in the short term (10-20 years) should be immediately incorporated into land use planning.

Second, for species facing unpredictable or discontinuous climate paths (due to physical barriers or climatic variability), the controversial strategy of ‘managed relocation’ may be more effective than corridors in achieving conservation objectives (Richardson *et al.* 2009). The efficacy of corridors versus managed relocation could be informed by climate-path analyses that consider measurements of the intrinsic life-history traits that will determine species’ range-shift ability (discussed above) and by regular population monitoring. If analyses suggest that an insurmountable gap will arise in the climate path, then the deterioration in viability within the species’ current range and suitability of conditions on the other side of the gap should be monitored concurrently. The combination of modelling and observation should then be used to inform decisions about whether to engage in managed relocation, as well as to determine the timing and location at which this approach would be most effective. Moreover, because climatic conditions in recipient locations might fluctuate considerably before becoming suitable for a target species, if managed relocation is enacted then relocated populations might need additional assistance to improve their likelihood of persistence.

Third, species’ range shifts and survival *in situ* could be aided by assisting extant populations to persist under future climatic variability. This could be achieved by mitigating against the impacts of climate change (e.g. via irrigation), by removing non-climatic stressors (such as predators or competitors), by improving habitat quality or connectivity (Grant *et al.* 2010), and through captive breeding programs or translocations of individuals to augment population size or genetic composition (Semlitsch 2000).

Conclusions:

Our climate-path analyses reveal a series of observations regarding climate-induced range dynamics that have previously received little attention. Variability in changing climate is likely to limit range expansions and shifts, and increase the likelihood of range contractions. The degree to which this occurs will strongly depend on species' ability to persist under short periods of unfavourable climate, as well as the more commonly recognised trait - dispersal ability. The relative importance of dispersal and persistence depend on the speed and regularity with which a climate path advances. Considering both traits in tandem is likely to be useful when developing region- and taxon-specific risk assessments. The net outcome of decadal range dynamics under climate change is increased endangerment for many species in our study and probable extinction for others. Assuming a steady rate of climate change to evaluate species' ability to shift their ranges may overestimate species' ability to shift their ranges. Although our results are based on a single taxonomic group from one region, we believe that our findings are generally applicable. The erratic tempo of climate change, which drives many of the complexities in range dynamics we observed, is likely to be a notable feature of many other parts of the world (Easterling *et al.* 2000; Fagre *et al.* 2003). Further refinement and application of climate-path analyses as suggested here would improve our ability to forecast

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

species’ responses to climate change and inform our use of alternative conservation strategies.

Acknowledgements:

We acknowledge the Program for Climate Model Diagnosis and Intercomparison (PCMDI) and the WCRP's Working Group on Coupled Modelling (WGCM) for making available the WCRP CMIP3 multi-model dataset. Support of this dataset is provided by the U.S. DOE. M. Tyree and T. Das at the UCSD climate research division assisted with interpretation of climate data. D. Wake gave advice on amphibian distributions and taxonomy. A. Weinblatt assisted with data management. F. Guilhaumon, V. St-Louis and C. Thomas commented on the manuscript. We greatly appreciate the input of three anonymous reviewers, which improved this manuscript.

References:

Anderson B.J., Akcakaya H.R., Araujo M.B., Fordham D.A., Martinez-Meyer E., Thuiller W. & Brook B.W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B-Biological Sciences*, 276, 1415-1420.

Anderson R.P. & Raza A. (2010). The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus <i>Nephelomys</i>) in Venezuela. *J. Biogeogr.*, 37, 1378-1393.

Aragón P., Lobo J.M., Olalla-Tárraga M.Á. & Rodríguez M.Á. (2009). The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography*, 19, 40-49.

Araújo M.B. & Luoto M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, 16, 743-753.

Araújo M.B., Nogues-Bravo D., Diniz-Filho J.A.F., Haywood A.M., Valdes P.J. & Rahbek C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, 31, 8-15.

Blaustein A.R., Belden L.K., Olson D.H., Green D.M., Root T.L. & Kiesecker J.M. (2001). Amphibian breeding and climate change. *Conservation Biology*, 15, 1804-1809.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Brooker R.W., Travis J.M.J., Clark E.J. & Dytham C. (2007). Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, 245, 59-65.

Carstens B.C., Stevenson A.L., Degenhardt J.D. & Sullivan J. (2004). Testing nested phylogenetic and phylogeographic hypotheses in the Plethodon vandykei species group. *Systematic Biology*, 53, 781-792.

Cayan D.R., Maurer E.P., Dettinger M.D., Tyree M. & Hayhoe K. (2008). Climate change scenarios for the California region. *Climatic Change*, 87, S21-S42.

Corn P.S. (2003). Amphibian breeding and climate change: Importance of snow in the mountains. *Conservation Biology*, 17, 622-625.

Corn P.S. (2005). Climate change and amphibians. *Anim. Biodivers. Conserv.*, 28, 59-67.

Coulson T., Catchpole E.A., Albon S.D., Morgan B.J.T., Pemberton J.M., Clutton-Brock T.H., Crawley M.J. & Grenfell B.T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292, 1528-1531.

Davidson C., Shaffer H.B. & Jennings M.R. (2002). Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. *Conservation Biology*, 16, 1588-1601.

Easterling D.R., Meehl G.A., Parmesan C., Changnon S.A., Karl T.R. & Mearns L.O. (2000). Climate extremes: observations, modeling, and impacts. *Science*, 289, 2068-2074.

Engler R. & Guisan A. (2009). MigClim: Predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, 15, 590-601.

Fagre D.B., Peterson D.L. & Hessl A.E. (2003). Taking the pulse of mountains: Ecosystem responses to climatic variability. *Climatic Change*, 59, 263-282.

Grant E.H.C., Nichols J.D., Lowe W.H. & Fagan W.F. (2010). Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proc. Natl. Acad. Sci. U.S.A.*, -.

Green D.M. (2003). The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, 111, 331-343.

Green D.M., Sharbel T.F., Kearsley J. & Kaiser H. (1996). Postglacial range fluctuation, genetic subdivision and speciation in the western North American spotted frog complex, Rana pretiosa. *Evolution*, 50, 374-390.

Hayes M.P. & Jennings M.R. (1986). Decline of Ranid Frog Species in Western North America: Are Bullfrogs (Rana catesbeiana) Responsible? *Journal of Herpetology*, 20, 490-509.

Hayhoe K., Cayan D., Field C.B., Frumhoff P.C., Maurer E.P., Miller N.L., Moser S.C., Schneider S.H., Cahill K.N., Cleland E.E., Dale L., Drapek R., Hanemann R.M., Kalkstein L.S., Lenihan J., Lunch C.K., Neilson R.P., Sheridan S.C. & Verville J.H. (2004). Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 12422-12427.

IUCN (2008). *IUCN Red List of Threatened Species*. [WWW document]. URL http://www.iucnredlist.org

Jackson S.T., Betancourt J.L., Booth R.K. & Gray S.T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, -.

Jiménez-Valverde A. & Lobo J.M. (2007). Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica*, 31, 361-369.

Kiesecker J.M., Blaustein A.R. & Belden L.K. (2001). Complex causes of amphibian population declines. *Nature*, 410, 681-684.

Kozak K.H. & Wiens J.J. (2006). Does niche conservatism promote speciation? A case study in north american salamanders. *Evolution*, 60, 2604-2621.

Kuchta S.R. (2007). Contact zones and species limits: Hybridization between lineages of the California Newt, Taricha torosa, in the southern Sierra Nevada. *Herpetologica*, 63, 332-350.

Maurer E.P., Brekke L., Pruitt T. & Duffy P.B. (2007). Fine-resolution climate projections enhance regional climate change impact studies. *Eos Trans*, 88, 504.

McMenamin S.K., Hadly E.A. & Wright C.K. (2008). Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 16988-16993.

Parmesan C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637-669.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing. In.

Reading C.J. (2007). Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, 151, 125-131.

Richardson D.M., Hellmann J.J., McLachlan J.S., Sax D.F., Schwartz M.W., Gonzalez P., Brennan E.J., Camacho A., Root T.L., Sala O.E., Schneider S.H., Ashe D.M., Clark J.R., Early R., Etterson J.R., Fielder E.D., Gill J.L., Minteer B.A., Polasky S., Safford H.D., Thompson A.R. & Vellend M. (2009). Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Sciences*, 9721-9724.

Root T.L., Price J.T., Hall K.R., Schneider S.H., Rosenzweig C. & Pounds J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57-60.

Russell R. (1926). *Climates of California*. University Press.

Semlitsch R.D. (2000). Principles for Management of Aquatic-Breeding Amphibians. *J. Wildl. Manage.*, 64, 615-631.

Smith M.A. & Green D.M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, 28, 110-128.

Soberon J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115-1123.

Steele C.A. & Storfer A. (2006). Coalescent-based hypothesis testing supports multiple Pleistocene refugia in the Pacific Northwest for the Pacific giant salamander (Dicamptodon tenebrosus). *Mol. Ecol.*, 15, 2477-2487.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Thuiller W. (2004). Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, 10, 2020-2027.

Thuiller W., Lavorel S., Araújo M.B., Sykes M.T. & Prentice I.C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8245-8250.

Vieites D.R., Nieto-Román S. & Wake D.B. (2009). Reconstruction of the climate envelopes of salamanders and their evolution through time. *Proc. Natl. Acad. Sci. U.S.A.*, 106, 19715-19722.

Waltari E., Hijmans R.J., Peterson A.T., NyÃ¡ri Ã.r.d.S., Perkins S.L. & Guralnick R.P. (2007). Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. *PLoS ONE*, 2, e563.

Walther G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2019-2024.

Walther G.R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.M., Hoegh-Guldberg O. & Bairlein F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389-395.

Wang G.L. & Schimel D. (2003). Climate change, climate modes, and climate impacts. *Annu. Rev. Environ. Resour.*, 28, 1-28.

Wiens J.A., Stralberg D., Jongsomjit D., Howell C.A. & Snyder M.A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U.S.A.*, 106, 19729-19736.

Williams J.W. & Jackson S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475-482.

Williams P., Hannah L., Andelman S., Midgley G., Araújo M., Hughes G., Manne L., Martinez-Meyer E. & Pearson R. (2005). Planning for climate change: identifying minimum-dispersal corridors for the Cape proteaceae. *Conservation Biology*, 19, 1063-1074.

ID	Species	Number of grid cells observed occupied between 1961-90.	False negative rate (composite model)	False positive rates (composite model)	Number of grid cells predicted suitable in 1961-90 (EOO)
1	*Ambystoma californiense*	34	0.05	1.26 / 0.17	328
2	*Aneides flavipunctatus*	83	0.14	0.74 / 0.11	268
3	*Batrachoseps gavilanensis*	43	0.07	0.20 / 0.15	148
4	*Batrachoseps gregarius*	45	0.02	0.30 / 0.28	76*
5	*Batrachoseps luciae*	20	0.10	0.83 / 0.40	105*
6	*Batrachoseps nigriventris*	75	0.13	0.70 / 0.26	233
7	*Dicamptodon ensatus*	24	0.00	0.68 / 0.15	75*
8	*Dicamptodon tenebrosus*	83	0.30	0.87 / 0.22	441
9	*Plethodon dunni*	33	0.18	0.88 / 0.10	233
10	*Rana boylii*	102	0.35	0.88 / 0.05	534

11	*Rana draytonii*	29	0.17	0.90 / 0.09	235
12	*Rana sierrae*	27	0.04	0.65 / 0.05	74*
13	*Rhyacotriton variegatus*	53	0.17	0.83 / 0.08	263
14	*Taricha sierrae*	27	0.00	0.74 / 0.27	104*
15	*Taricha torosa*	47	0.15	0.83 / 0.04	230

Table 1.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Parameters:	Parameter description:
Low dispersal	Species can colonise any or all of the eight cells surrounding it if cells are climatically suitable (~12km / decade)
High dispersal	Species can colonise any or all of the 20 cells surrounding it (~24 km / decade)
No persistence under unsuitable climates	Species disappear from a cell as soon as climate suitability drops below the species-specific threshold
One/two decade/s persistence under unsuitable climates	Species persist in a cell for one/two decade/s after climate becomes unsuitable, and are able to colonise other cells during those decades

Table 2.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

Table Legends:

Table 1. Species identities and performance metrics for the individual and composite GAM bioclimate models. There are two false positive rates for each species: the first was calculated using grid cells observed to be occupied, the second using expert-defined ranges and excluding non-seeded false positives (see methods). *Current IUCN status (based solely on number of cells predicted suitable) is ‘Vulnerable’.

Table 2. Parameters used to model species’ ability to shift their geographic ranges.

Figures:

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

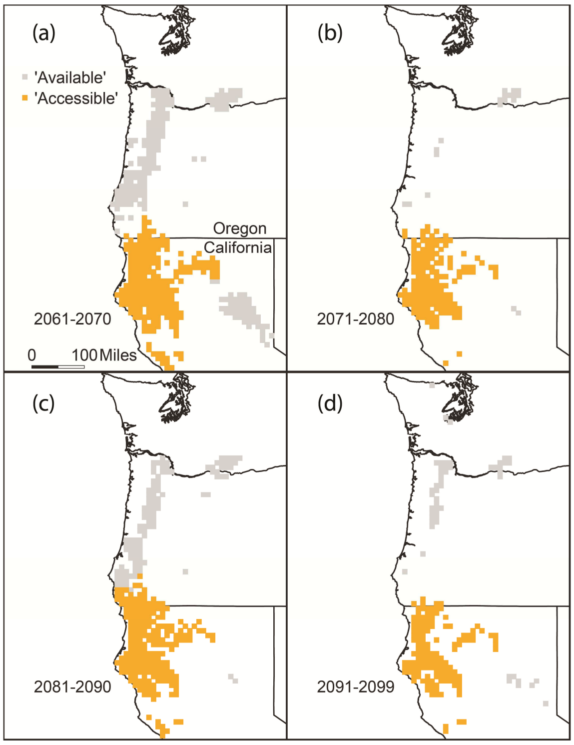

Figure 1. Range dynamics and the formation of a climate path “gap” for *Aneides flavipunctatus* during four consecutive decades of climate change (predicted using HCM, scenario B1). Orange squares (‘accessible’): the portion of suitable climate space that could be occupied assuming high dispersal and one decade persistence under unsuitable climates. Grey squares (‘available’): potential climate niche that does not become occupied. The coastline and states of California (most southerly), Washington (most northerly) and Oregon (intermediate) are outlined in black.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

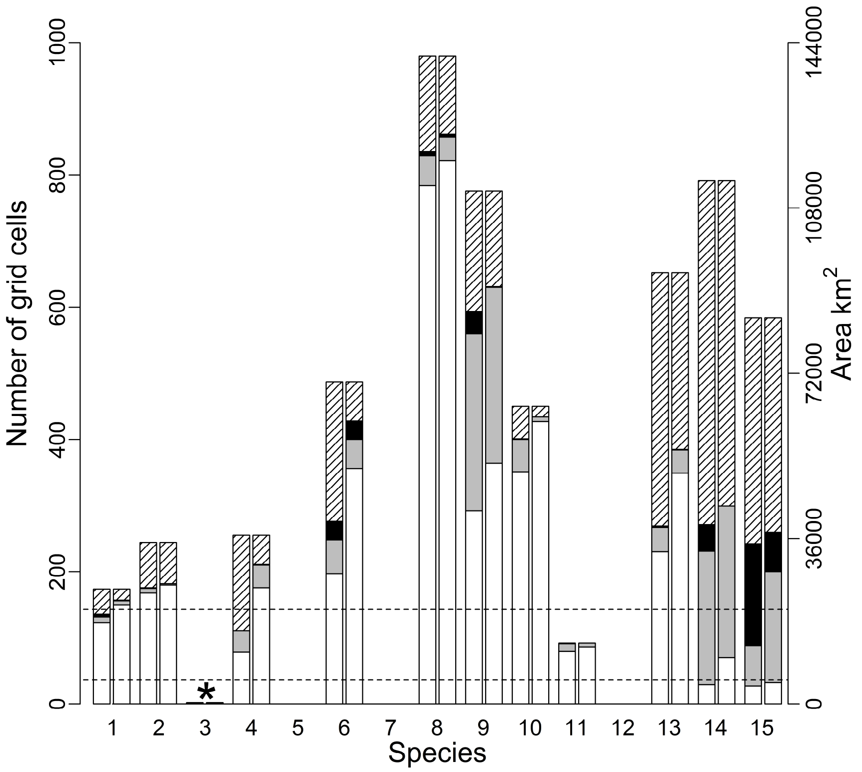

Figure 2. Mean predicted extent of occurrence (EOO) between 2071 and 2099 for each species under HCM, scenario B1 (see Table 1 for species identity and current IUCN status). Each pair of bars represents EOO under low (left bar) and high (right bar) dispersal for each species. White bar segments represent no persistence under unsuitable climate, grey segments represent one decade persistence, and black segments represent two decades persistence. Hatched segments represent EOO if the species could disperse to all suitable climate space. Dashed horizontal lines represent EOO threshold criteria for IUCN red list statuses. 'VU': Vulnerable, 'EN': Endangered. A species occupying a single grid cell is classed as 'Critically Endangered' and is signified by an asterisk. Three species (ID # 5, 7 and 12) are predicted to have no suitable climate space under HCM B1.

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

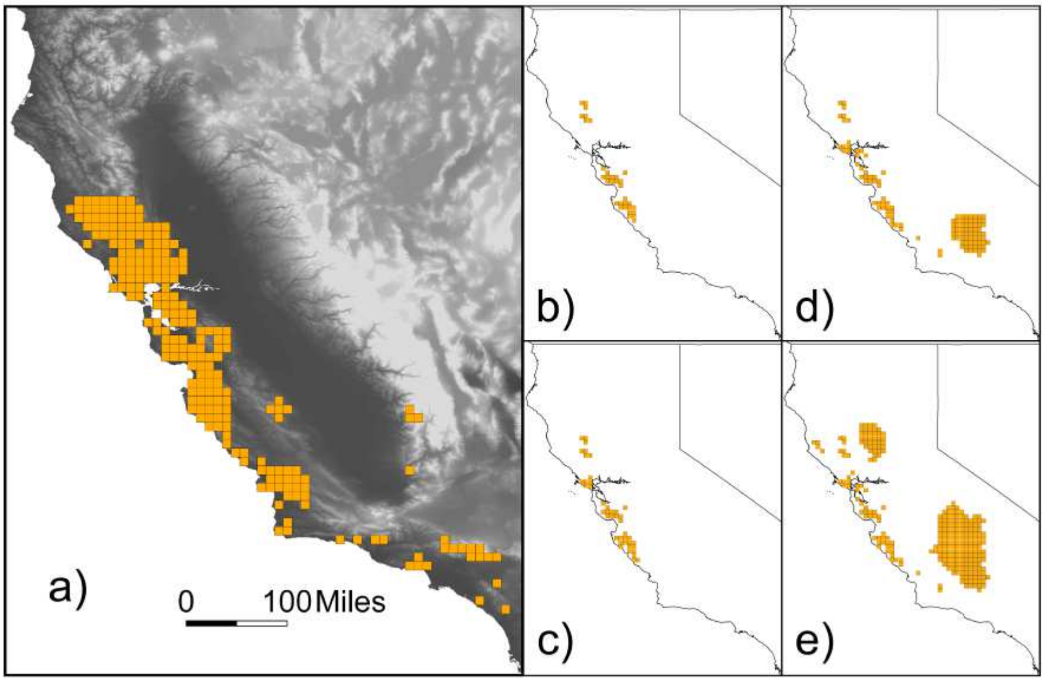

Figure 3. The interplay of dispersal ability and persistence in limiting the amount of climate space occupied by *Taricha torosa*. a) Orange shading: 1961-90 climatically suitable range. Greyscale shading: topography (white = high elevation, black = low elevation). b-e) The portion of the 2091-2099 climate space (predicted using HCM, scenario B1) that could be occupied assuming: b) low dispersal, no persistence; c) high dispersal, no persistence; d) low dispersal, one decade persistence; e) high dispersal, one decade persistence. The coastline (west) and California and Nevada state borders are outlined in black.

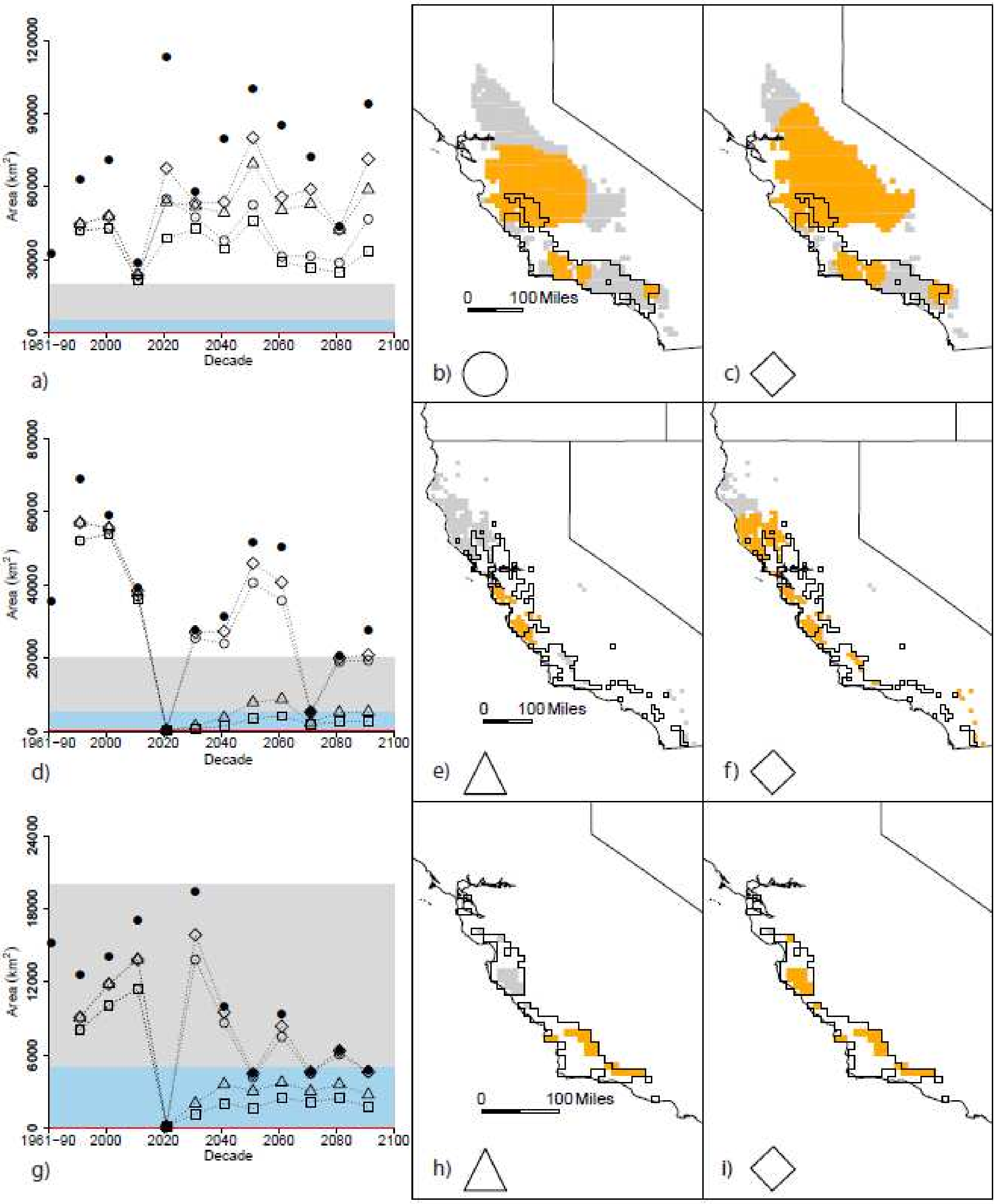

Figure 4. Range shift predictions for three species in California ((a-c) *Batrachoseps nigriventris* (predicted using HCM, scenario B1), (d-f) *Rana draytonii*, (g-i) *Batrachoseps luciae*, (range shifts of *R. draytonii* and *B. luciae* predicted using PCM, scenario A2)) under different survival and dispersal scenarios. (a,d,g) Predicted potential and actual range sizes each decade from 1990-2099. Filled circles

Accepted for publication: Early, R. and D. F. Sax (2011). "Analysis of climate paths reveals potential limitations on species range shifts." Ecology letters **14**(11): 1125-1133.

= potential range size based on the amount of suitable climate space available.

Empty symbols = actual area occupied given: diamonds – high dispersal, one decade persistence; triangles – high dispersal, no persistence; circles – low dispersal, one decade persistence; squares - low dispersal, no persistence. (b,c,e,f,h,i) Outlined space: 1961-90 suitable climate space; grey: suitable climate space in 2091-99 that does not become occupied; orange: the portion of the 2091-2099 suitable climate space that could be occupied given parameter combinations corresponding to the symbol in the lower left of the panel. The coastline (west) and border between California and Nevada (east) are outlined in black.