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4 Analysis of climate paths reveals potential limitations on species range shifts
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6 **Running title:**
7 Climate paths
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1   **Abstract**.

2   Forecasts of species endangerment under climate change usually ignore the

3   processes by which species ranges shift. By analysing the 'climate paths' that range

4   shifts might follow, and two key range-shift processes - dispersal and population

5   persistence - we show that short-term climatic and population characteristics have

6   dramatic effects on range-shift forecasts. By employing this approach with 15

7   amphibian species in the western USA, we make unexpected predictions. First, inter-

8   decadal variability in climate change can prevent range shifts by causing gaps in

9   climate paths, even in the absence of geographic barriers. Second, the hitherto

10   unappreciated trait of persistence during unfavourable climatic conditions is critical

11   to species range shifts. Third, climatic fluctuations and low persistence could lead to

12   endangerment even if the future potential range size is large. These considerations

13   may render habitat corridors ineffectual for some species, and conservationists may

14   need to consider managed relocation and augmentation of *in situ* populations.

15

16   **Introduction:**

17

18   Climate change has contributed to pronounced changes in the geographic distribution

19   of species over the past several decades (Walther *et al.* 2002; Root *et al.* 2003;

20   Parmesan 2006). Over the remainder of this century, climate change is expected to

21   cause many more species' ranges to shift, collapse or expand - leading to a major

22   reorganization of ecological communities and biodiversity loss (Walther 2010). The

23   predominant approach for forecasting species' range-responses to climate change

1   uses climate at the locations a species currently occupies to evaluate the temperature

2   and precipitation conditions that permit a positive net population growth rate, i.e.,

3   bioclimatic niche modelling (Soberon 2007). These bioclimate models are then used

4   to predict the geographic locations that the species could potentially occupy at some

5   point in the future, and risk assessments are based on assumptions about the species'

6   ability to shift its range to these locations. For example, it may be assumed that a

7   species cannot disperse beyond its current range or alternatively that it can disperse

8   to any place that will be climatically suitable for it (e.g. Thuiller *et al.* 2005). These

9   assumptions can be used to estimate the extremes of extinction likelihoods, but

10   provide no insight into the actual range dynamics that will play-out during range

11   shifts.

12

13   Here we map the 'climate paths' along which species' ranges may shift, i.e. the paths

14   formed by the location of places with suitable climatic conditions during a sequence

15   of time steps. We use measures of dispersal and population persistence to predict

16   range dynamics along these paths. Most previous analyses of this kind have assumed

17   an evenly graduated change in climate, which would facilitate gradual and steady

18   range shifts (Brooker *et al.* 2007; Anderson *et al.* 2009). In reality, climate change is

19   likely to be highly dynamic, with short-term fluctuations both above and below a

20   directional trend (Easterling *et al.* 2000; Wang & Schimel 2003). This may cause

21   species to colonise new areas during episodic warm periods, and to pause or

22   temporarily retreat during cool periods (Walther *et al.* 2002; Jackson *et al.* 2009). In

23   such an environmental regime, range expansions would be aided if populations could

1   survive short periods when climate is unfavourable for them. This would prevent

2   ranges from contracting during cool episodes. Then, when conditions improve,

3   populations that survived at a range margin would produce dispersing individuals

4   that could further extend the species' range (Jackson *et al.* 2009). Range expansion

5   rates would also increase with the distance that individuals could disperse in a given

6   time step (Anderson *et al.* 2009). Range-shift predictions have only recently begun to

7   consider dispersal (Williams *et al.* 2005; Anderson *et al.* 2009; Engler & Guisan

8   2009), and to our knowledge persistence and climate variability have yet to be

9   considered explicitly. We investigate the importance of these processes using 15

10   amphibian species endemic to the western USA, for the time period between 1990

11   and 2100.

12

13   Limited empirical data on population processes often restrict the scope of range-

14   dynamic forecasts to a few, well studied species (Anderson *et al.* 2009; Engler &

15   Guisan 2009). We circumvent this limitation by 'experimenting' with different

16   values for species' traits. This yields principles regarding the relative importance of

17   persistence and dispersal, given the different ways in which climate paths might

18   advance, that are widely applicable outside this study system.

19

20   **Material and Methods:**

21

22   Species distribution data - We conducted analyses for amphibian species whose

23   entire range lies west of the 100th meridian – amphibian ranges rarely cross this

1   meridian, which divides the Rocky mountains and Great Plains from the east of the

2   USA. Of these species we used only those whose ranges fall entirely within USA

3   borders and for which sufficient bioclimate modelling data were available (15

4   species). Species point occurrences from 1961-90 were taken from Global

5   Biodiversity Information Facility (http://www.gbif.org). Occurrences that could not

6   be confidently geo-referenced were discarded. We used the most current

7   phylogeographic studies to assign location records to the correct species (S1).

8   Species range polygons were taken from the IUCN Red List website (IUCN 2008).

9

10   Climate variables - Bioclimate models were built using means from 1961-90 of the

11   following variables: mean annual temperature, mean temperature of the coldest

12   month, mean temperature of the hottest month, mean annual precipitation, mean

13   monthly winter precipitation (January to March) and mean monthly summer

14   precipitation (June to August). These variables reflect critical periods in the life

15   history of west coast amphibians. Winter precipitation and temperature govern

16   snowfall, snowmelt and hydroperiod, which in turn affect success of aquatic

17   reproduction and terrestrial breeding behaviour (Blaustein *et al.* 2001; Corn 2003;

18   McMenamin *et al.* 2008). Summer precipitation and temperature are linked to larval

19   and adult mortality (Corn 2005). Range shifts were projected using predictions from

20   the Hadley CM3 (HCM) and PCM3 (PCM) General Circulation Models (GCMs)

21   throughout the period 1991-2100, using A2 and B1 emissions scenarios. Climate

22   predictions that were bias-corrected and spatially downscaled (to 1/8º, approximately

1 140 km^2, resolution) as described by Maurer et al (2007) were taken from http://gdo-

2 dcp.ucllnl.org/downscaled_cmip3_projections/.

3

4 Bioclimate modelling - For our focal species, we evaluated the utility of four

5 bioclimate modelling techniques: Generalized additive model (GAM), Mahalanobis

6 distances, Bioclim and Maxent (S1). Of these approaches, GAMs minimized false

7 presences and absences creating the most reliable models for most species (S1) and

8 we thus base our results on a GAM approach. We used species occurrence points to

9 construct GAMs using thin plate regression splines and Generalised Cross Validation

10 (GCV). We multiplied the degrees of freedom in the GCV score by 1.4 to create

11 smoother models, in light of the small number of species occurrences (Table 1).

12 Since no absence data were available, we randomly sampled pseudo-absences (twice

13 as many as the number of presences for each species) from the 1500 cells (~210000

14 km^2, a region with radius ~ 150km) surrounding the cells a species occurred in. See

15 S1 for further details on the choice of sample region. Cells classed as pseudo-

16 absences could in fact be climatically suitable. This, combined with the small

17 number of records, reduced our confidence in an individual model's ability to

18 accurately discriminate between suitable and unsuitable climatic conditions.

19 Therefore, we repeated the pseudo-absence sampling process to build 100 bioclimate

20 models for each species. If one of the 100 GAM algorithms could not converge on a

21 single model it was discarded and a new set of pseudo-absences were sampled. The

22 consistency (correlation) between these models reflects the degree to which each

23 species' climate niche is genuinely distinct from the surrounding environment. For

1   1961-90 and decadal future climates, we calculated the mean suitability predicted for

2   each grid cell by all 100 models, to produce a composite suitability map.

3

4   We classified cells as suitable or unsuitable according to a species-specific threshold

5   that minimised the difference between sensitivity and specificity within the sample

6   region. This approach weights omission and commission errors equally and is

7   amongst the most accurate of thresholding techniques (Jiménez-Valverde & Lobo

8   2007). In a few cases we manually altered thresholds (S1). Model performance was

9   assessed using deviance explained, AUC and false positive and false negative rates.

10 The number of false positives was calculated in two ways. First we summed the

11 number of grid cells west of the 100th meridian that were predicted to be suitable but

12 which were not occupied. The false positive rate was calculated using the number of

13 point occurrences for each species as the denominator rather than the number of

14 absences, so as to demonstrate the degree of over-prediction relative to current range

15 size. This false positive rate might be high even for accurate models, because under-

16 recording can mistakenly lead to the appearance of false positives and because

17 suitable climate space may exist too far from a species' range to be occupied. Thus,

18 secondly we calculated the number of grid cells that were predicted to be suitable but

19 which fell outside the expert-defined range polygons (IUCN 2008) and were

20 'seeded' using the criteria listed below. False positive rates were calculated for these

21 data using the number of grid cells in the species range polygon as the denominator.

22 Statistical analyses were conducted in R 2.9.2 (R Development Core Team 2009)

23 incorporating the ROCR and mgcv packages.

1

2   Climate-path modelling - To construct climate paths we predicted the 1/8º grid cells

3   predicted to be suitable for each species during each decade between the years 1991

4   and 2100 ('climate space'). Decadal climate values were taken from the emissions

5   scenario, averaged across the decade. We then simulated species progress along

6   these climate paths each decade by implementing rules governing dispersal and

7   persistence, as described in Table 2. Simulations were begun ('seeded') using all

8   grid cells predicted suitable in 1961-90, excluding grid cells that were geographically

9   disjunct from the species observed range (point occurrences and polygon) by more

10   than six grid cells, or that were less geographically disjunct but were occupied by a

11   congener known to competitively exclude the focal species. Thus, although areas

12   distant from a species' current range might be predicted to be suitable, they would

13   not influence the starting point of climate path simulations.

14

15   Predicting IUCN status – For comparability, current and projected future IUCN

16   statuses were calculated using the 'Extent of Occurrence' (EOO) criteria alone

17   (Critically Endangered: $< 100 km^2$, Endangered: $< 5000 \ km^2$, Vulnerable

18    $<20000 km^2$). Current EOO was calculated as the sum of the area of the cells that

19   were climatically suitable between 1961-90. Statuses calculated from current EOO

20   differed from IUCN statuses only if the IUCN status also considered population

21   decline and habitat quality. Future EOOs were calculated as the mean area of the

22   cells that were predicted to be occupied in the decades 2071-2099.

23

1 **Results**

2

3 Our analysis of climate paths revealed three key observations relevant to range

4 dynamics under climate change.

5

6   1. Gaps in the climate path.

7 Given likely dispersal and persistence parameters, fluctuations around the directional

8 trend of climate change can create gaps in climate paths. These gaps can prevent

9 species from reaching climatically suitable regions, even in the absence of physical

10 barriers to dispersal. Physical features, such as mountain ranges or desert regions can

11 form barriers to range shifts because they contain areas that will not become

12 climatically suitable for a given species over the time-scale of interest (Engler &

13 Guisan 2009). However, gaps arise if some critical portion of a climate path is only

14 available at a time step in which a species is unable to pass through it. For example,

15 *Aneides flavipunctatus* may be unable to shift into its full potential future range

16 because climate variability after 2050 causes the landscape connecting northern

17 California and southern Oregon to become climatically suitable only transiently. This

18 leaves insufficient time for the species to pass through the area (Fig. 1). Assuming

19 different parameters made almost no difference to this outcome (Fig. 2). Graphs of

20 the potential and occupied range size reveal the instances in which climatic

21 fluctuations prevent progress along the climate path (S2). All species we examined

22 showed at least some evidence that they will be unable to fully occupy the entire

23 climate space projected to be available to them by 2100 because of a combination of

9

1   permanent climatic barriers and temporary gaps in the climate path (Fig. 2, S2&4).

2   Indeed, most species (11 of 15) are projected to occupy less than half of their

3   available climate space by 2100 under at least some of the examined climate change

4   and population parameter values (Fig. 4, S2 & 4).

5

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

7   The ability to persist during short periods of unfavourable climate can be as

8   important as dispersal ability in determining whether species can shift their range

9   along a climate path and avoid range collapse. For example, the range-shift distance

10   and range size of *Taricha torosa* in 2100 is more strongly increased by persistence

11   during a single decade of unfavourable climate than it is by our high dispersal

12   parameter (in which colonisation could occur across 24km/decade) (Fig. 3). This is

13   the case for many other species (Fig. 2, S2-4).

14

15   The relative importance of dispersal and persistence depends on the dynamics of the

16   climate path. For example, the climate path of *Batrachoseps nigriventris* advances

17   fairly steadily (S3). High dispersal allows *B. nigriventris* to shift northwards every

18   decade, regardless of its persistence ability (Fig. 4a-c). However, if the climate path

19   advances jerkily, often retreating, the relative importance of dispersal and persistence

20   is flipped. For example, dispersal ability affects *Rana draytonii*'s progress along the

21   climate path very little, but the ability to persist in place through one decade of

22   unfavourable climate makes the difference between range collapse and range shift

23   (Fig. 4d-f, S3). Both dispersal and persistence also affect outcomes for species whose

1   ranges do not shift along a climate path but remain in place or collapse. For example,

2   the climate space of *Batrachoseps luciae* does not shift, but shrinks by 2100. *B.*

3   *luciae* continues to occupy a wider proportion of its potential range throughout the

4   21st century given high dispersal and short-term persistence than without short-term

5   persistence (Fig. 4g-i).

6

7   3. Future endangerment is not necessarily commensurate with species' future

8   potential range size

9   Although none of the species examined are currently classed as Endangered or

10   Critically Endangered, some species are likely to become endangered because their

11   suitable climate space is projected to decrease (Fig. 2). However, we predict that

12   many species will become endangered even though they are projected to have large

13   areas of suitable climate space in 2100 (Fig. 2). These species decline because they

14   are unable to shift into their future potential range due to gaps in the climate path

15   caused by climatic fluctuation. These declines occur irrespective of the climate

16   forecasts used, although there is variation in the precise number and identity of

17   species in each risk category (S4). Species' available climate space is smaller on

18   average under HCM (the General Circulation Model that indicates the greatest

19   temperature increase) than PCM. For example, one species loses all climate space

20   under PCM (A2 and B1), whilst three or four species lose all climate space under

21   HCM (A2 and B1 respectively, Fig. 2, S4). However, under low dispersal and no

22   persistence three species become Critically Endangered under PCM A2 and B1,

23   despite there being sufficient available climate space for them to remain Endangered

1   or Least Concern. Under HCM A2 and B1 zero and two species respectively become

2   Critically Endangered. Evidence that it is climatic fluctuation which limits range

3   shifts in PCM climate forecasts comes from the effect of persistence. Allowing

4   species to persist during periods of unfavourable climate had a significantly greater

5   effect on the proportion of climate space that becomes occupied under PCM than

6   under HCM (given low dispersal: paired t test, p=0.040 and p=0.015 for one or two

7   decades persistence respectively), whereas the effect of increasing dispersal was not

8   significantly different between HCM and PCM.

9

10   **Discussion**

11

12   Climate path analyses find that range shifts, expansions and contractions can be

13   greatly affected by climatic variability, causing persistence to have a strong effect on

14   whether species shift their ranges, and having unexpected and important implications

15   for conservation plans. Climate paths evaluate the routes along which species ranges

16   might move by dividing range shifts into time steps. The time steps used (decades in

17   our analyses) reflect both the length of time over which the focal species could

18   disperse and establish new populations, and the periodicity of the natural climatic

19   oscillations within the study region. Climate forecasts cannot capture the spatial and

20   temporal pattern of climate change with sufficient accuracy to predict the exact

21   timing or location of range shifts. Instead, the purpose of the approach we suggest is

22   to investigate how the spatio-temporal pattern of climate change places extrinsic

23   limitations on species' ability to shift their ranges. This gives us insight into how

1 species' intrinsic traits might interact with the pattern of climate change to drive

2 range dynamics. Below we discuss how the processes we investigate interact with

3 each other and with other range-shift limitations.

4

5 <u>Intrinsic traits that determine species' shifts along the climate path:</u>

6 Recent research has found that dispersal ability can affect range-shift potential (e.g.

7 Anderson *et al.* 2009; Engler & Guisan 2009), but to our knowledge this is the first

8 time that the importance of persistence under short-term unfavourable climate

9 conditions has been quantified. The degree of persistence that is required to prevent

10 an advancing range margin from retreating when climate is poor depends on the

11 degree and periodicity of climate variability. In our system, persistence for a single

12 decade often had a strong effect because climatic fluctuations were strongly decadal

13 (fig. 2, S4, Wang & Schimel 2003). Increasing persistence for a further decade

14 tended to have a smaller effect, since periods of unfavourable conditions rarely

15 existed in two contiguous decades. An important exception was *Taricha sierrae*

16 under PCM A2, which did not survive at all given one decade persistence, but which

17 remained 'Vulnerable' given two decades persistence regardless of dispersal ability

18 (S4). The other notable exception was *T. torosa* under HCM B1 whose future range

19 size given low dispersal was more than doubled by two decades persistence,

20 producing almost the same result as high dispersal and two decades persistence (Fig.

21 3).

22

1   Persistence will be determined by species' population demography, physiology and

2   behaviour (e.g. occupying ameliorative microclimates) (Coulson *et al.* 2001; Green

3   2003; Reading 2007). For these amphibians we believe that persistence outside of

4   their climatic tolerances for more than two decades is unlikely. Their longevity is not

5   well understood but most appear to be reproductively active for less than a decade,

6   and in addition to climate change their populations are threatened by non-climatic

7   environmental stressors including habitat destruction, agricultural pollution,

8   pathogens and invasive species (Hayes & Jennings 1986; Kiesecker *et al.* 2001;

9   Davidson *et al.* 2002). The importance of the interaction between climatic

10   variability, dispersal and persistence has been recognised theoretically (Jackson *et al.*

11   2009) but rarely examined in practice. Given the importance of persistence in driving

12   range dynamics within this study and the global predictions of variability in the rate

13   of climate change (Easterling *et al.* 2000; Wang & Schimel 2003), we recommend

14   that collecting data on these traits should be an urgent priority.

15

16   Despite our emphasis on persistence, dispersal remains important for range-shifts.

17   Dispersal ability is most important when the climate path moves steadily (*B.*

18   *nigriventris*, Fig. 4a-c), and can interact strongly with persistence when the climate-

19   path steps are large and uneven (*T. torosa*, Fig. 3). For the species we considered,

20   our high dispersal parameter of 24km/decade is probably overly-optimistic. The

21   majority of the species we studied are highly philopatric salamanders and newts,

22   which have been recorded at a maximum of a few hundred metres from their home

23   site (Smith & Green 2005). The other species are anurans, which can travel multiple

1   kilometres, but are rarely expected to achieve 24km of dispersal in a single decade

2   (Smith & Green 2005). For both groups, these dispersal distances are based on

3   seasonal breeding migrations and there is no evidence this behaviour would facilitate

4   migrations to new breeding areas. If maximum dispersal distances per decade are

5   less than 12 km/decade (our low dispersal parameter), which is not unlikely for some

6   species, then range collapse and extinction should be more common then we predict.

7   Low average rates of dispersal may be bolstered by rare long-distance dispersal

8   events (Engler & Guisan 2009). This would likely improve many of our species'

9   range-shift abilities, given the gaps that appeared in their climate paths (Figs. 1 & 3).

10 However, even less information is available with which to parameterise such

11 occurrences than for average dispersal. We recommend that the triggers leading to

12 dispersal and breeding outside the natal range, as well as the length of these dispersal

13 events, become research priorities - as only this type of dispersal will drive range

14 shifts.

15

16 Unanticipated consequences of climate forecasting technique:

17 We used two General Circulation Models, both thought to accurately represent

18 climatic patterns across most of the study region (PCM and HCM3, Cayan *et al.*

19 2008), in order to bracket the range of possible outcomes. PCM is least sensitive to

20 greenhouse gas forcing and shows the least overall climate change (Hayhoe *et al.*

21 2004). Thus, species' climate niches tend to move shorter geographic distances under

22 PCM than under HCM (S3). However, the PCM model still predicts considerable

23 fluctuations in precipitation in the study region. In fact, under some combinations of

1   modelled conditions, PCM can even result in more Endangered and Critically

2   Endangered species than HCM as climatic fluctuations make it harder for species to

3   shift or maintain their range (Fig. 2, S4). Therefore it is not solely the directional

4   magnitude of predicted climate change that is important; an increase in climatic

5   variability could cause range collapse and inhibit range shifts.

6

7   An important note is that the climate change data used here are the average of

8   multiple climate change simulations, and so are somewhat smoothed. Thus, in reality

9   climate change may be even more variable, and persistence even more important

10 than our estimates suggest.

11

12 The two greenhouse gas emission scenarios we used represent conservative (B1) and

13 extreme (A2) estimates (Hayhoe *et al.* 2004). We have largely discussed examples

14 using the B1 scenario in order to demonstrate that our findings are not simply caused

15 by extreme climate predictions. Interestingly, outcomes under the A2 scenario are

16 not always worse than under B1. For example, for *Taricha torosa* the higher degree

17 of warming predicted under A2 created more future climate space than under B1

18 (S2). If *T. torosa* could reach this climate space then A2 might be less deleterious

19 than B1.

20

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

22 Both the presence of negative and absence of positive biotic interactions limit

23 species current ranges and are likely to reduce the area and continuity of the climate

16

1   path (Araújo & Luoto 2007; Wiens *et al.* 2009). Consider, for example, what would

2   happen if the climate paths of two competitor species coincide. Even if these species

3   can co-exist at the landscape scale, at fine scales the presence of a competitor species

4   will likely impede the establishment and the eventual size and number of populations

5   of one or both species. Small, scarce populations produce few dispersing individuals

6   and are poorly able to persist during unfavourable climates. Hence we expect that

7   competition at fine scales would amplify gaps in species' climate paths. Such a

8   situation is possible for at least one species in our analysis: *T. torosa*'s climate path

9   takes it into the Sierra Nevada Mountains of eastern California (Fig. 2) where the

10   closely related species *T. sierrae* is incumbent (Kuchta 2007).

11

12   The broad resolution of our analyses ensured that our predictions were based on

13   general climatic trends, rather than local climatic predictions that are too specific to

14   be realistic. However, at fine scales, species' vegetation, hydrology and microclimate

15   requirements will likely limit the area and continuity of the climate path. In

16   particular, anthropogenic landscape modification could form significant range-shift

17   barriers. For example, *T. torosa* may need to cross the northern portion of the

18   agriculturally intensive Central Valley (Fig. 3). This fragmented landscape will not

19   only pose dispersal barriers but will reduce population size and thus persistence.

20   Thus by restricting both dispersal and persistence, habitat fragmentation may be even

21   more deleterious to range shifts than previously recognised.

22

23   Bioclimate models:

17

1   Calculating a species' climatic niche by correlating its locations with underlying

2   climate data is subject to serious criticisms. One criticism is that these models

3   assume that the species' distribution is in equilibrium with its environment and is not

4   prevented from filling its entire niche, for example by dispersal limitations or biotic

5   interactions (Soberon 2007; Wiens *et al.* 2009). While we cannot rule out the

6   importance of this criticism in full, we have several reasons to believe that this

7   criticism is of limited importance for the species we modeled. First, the composite

8   GAMs we constructed seem well supported by the finding that the climate niches

9   predicted were closely tied to distinct climate zones in California; for example the

10   'Hot Mediterranean' climate zone in western Sierra Nevada for *T. sierrae* and 'Hot

11   Steppe' grassland for *Batrachoseps gregarious* (climate classifications from Russell

12   1926). Second, the models generally explained large quantities of deviance, had low

13   omission rates and the area they predicted to be suitable coincided well with the

14   expert-defined range (Table 1, S1). However, *Dicamptodon tenebrosus and Rana*

15   *boylii* had high apparent omission rates. These rates are due to isolated populations

16   and competitive interactions that exclude species from part of their climatically

17   suitable range; nevertheless, these species' bioclimate models actually performed

18   rather well (for further explanation see S1). Third, there was a good degree of

19   overlap between multiple GAMs (S1). This suggests that species we studied

20   genuinely occupy specific climate niches that are unique within the surrounding

21   landscape. Finally, whilst performing more 'accurately' than the other approaches

22   tested, composite GAMs predicted similar amounts of range loss and climate path

1 variability to these approaches (S1). Thus our climate path results are unlikely to be

2 artifacts of the modelling technique.

3

4 A second criticism is that bioclimate models assume that species cannot live under

5 combinations of climatic variables that are different from those they currently

6 occupy, i.e. 'no-analog climates' (Williams & Jackson 2007). It has been suggested

7 that during the Pleistocene some North American amphibian species occupied

8 climatic conditions that were not analogous to the species' current range (Waltari *et*

9 *al.* 2007). However, the refugia in which this occurred were in areas that were cooler

10 and wetter than species' current climate niches (Waltari *et al.* 2007). Precipitation is

11 particularly important to amphibian distributions (Aragón *et al.* 2009), with effects

12 on seasonal breeding habitat and food sources (Corn 2003, 2005). Precipitation

13 change is predicted to change the hydrology of the study region substantially (Cayan

14 *et al.* 2008). Therefore, persistence of the study species for long periods in the future

15 under hotter, drier conditions than they currently experience seems more unlikely

16 than in previous cooler, wetter conditions.

17

18 A third criticism is that species may adapt to changing climatic conditions, allowing

19 them to survive in place (Wiens *et al.* 2009). This seems unlikely to be the case for

20 our study organisms as a considerable amount of research has found little change in

21 amphibian climatic niches over long periods of climate change (e.g. Kozak & Wiens

22 2006; Waltari *et al.* 2007; Vieites *et al.* 2009). Amphibian range shifts driven by

1   Pleistocene climate change are common globally and within the study region (Green

2   *et al.* 1996, Carstens *et al.* 2004; Steele & Storfer 2006; Araújo *et al.* 2008).

3

4   Regardless of these arguments, the ability of bioclimate models to predict into new

5   time periods can rarely be tested. Consequently, we do not suggest that the species-

6   specific predictions made here will be accurate, but instead that these models are

7   sufficiently robust to demonstrate the likely scope of the species' range-dynamic

8   responses to climate change.

9

10   <u>Implications for Conservation Management:</u>

11   We discuss three key management implications of our findings. First, constraints

12   imposed by climatic variability, limited dispersal and low persistence may mean that

13   even habitat corridors through high-quality habitat may not in themselves make

14   range shifts possible. Additionally, corridors for species that show high uncertainty

15   between climate paths under different GCMs are less likely to be effective. Where

16   corridors are appropriate, their effectiveness will depend on how well the corridor

17   landscape facilitates population persistence in addition to dispersal. Species' range

18   shifts along corridors could be expedited by assisting or augmenting populations that

19   'naturally' establish themselves along the corridor. Given current uncertainty in

20   climate modelling, predictions of climate paths many decades into the future may be

21   an inadequate basis for corridor planning. However, the predicted directionality of

22   range shifts in the short term (10-20 years) should be immediately incorporated into

23   land use planning.

1

2   Second, for species facing unpredictable or discontinuous climate paths (due to

3   physical barriers or climatic variability), the controversial strategy of 'managed

4   relocation' may be more effective than corridors in achieving conservation

5   objectives (Richardson *et al.* 2009). The efficacy of corridors versus managed

6   relocation could be informed by climate-path analyses that consider measurements of

7   the intrinsic life-history traits that will determine species' range-shift ability

8   (discussed above) and by regular population monitoring. If analyses suggest that an

9   insurmountable gap will arise in the climate path, then the deterioration in viability

10   within the species' current range and suitability of conditions on the other side of the

11   gap should be monitored concurrently. The combination of modelling and

12   observation should then be used to inform decisions about whether to engage in

13   managed relocation, as well as to determine the timing and location at which this

14   approach would be most effective. Moreover, because climatic conditions in

15   recipient locations might fluctuate considerably before becoming suitable for a target

16   species, if managed relocation is enacted then relocated populations might need

17   additional assistance to improve their likelihood of persistence.

18

19   Third, species' range shifts and survival *in situ* could be aided by assisting extant

20   populations to persist under future climatic variability. This could be achieved by

21   mitigating against the impacts of climate change (e.g. via irrigation), by removing

22   non-climatic stressors (such as predators or competitors), by improving habitat

23   quality or connectivity (Grant *et al.* 2010), and through captive breeding programs or

1   translocations of individuals to augment population size or genetic composition

2   (Semlitsch 2000).

3

4   Conclusions:

5   Our climate-path analyses reveal a series of observations regarding climate-induced

6   range dynamics that have previously received little attention. Variability in changing

7   climate is likely to limit range expansions and shifts, and increase the likelihood of

8   range contractions. The degree to which this occurs will strongly depend on species'

9   ability to persist under short periods of unfavourable climate, as well as the more

10   commonly recognised trait - dispersal ability. The relative importance of dispersal

11   and persistence depend on the speed and regularity with which a climate path

12   advances. Considering both traits in tandem is likely to be useful when developing

13   region- and taxon-specific risk assessments. The net outcome of decadal range

14   dynamics under climate change is increased endangerment for many species in our

15   study and probable extinction for others. Assuming a steady rate of climate change to

16   evaluate species' ability to shift their ranges may overestimate species' ability to

17   shift their ranges. Although our results are based on a single taxonomic group from

18   one region, we believe that our findings are generally applicable. The erratic tempo

19   of climate change, which drives many of the complexities in range dynamics we

20   observed, is likely to be a notable feature of many other parts of the world

21   (Easterling *et al.* 2000; Fagre *et al.* 2003). Further refinement and application of

22   climate-path analyses as suggested here would improve our ability to forecast

1   species' responses to climate change and inform our use of alternative conservation

2   strategies.

3

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5

15

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30

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

1
2   Table 1.

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.

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:
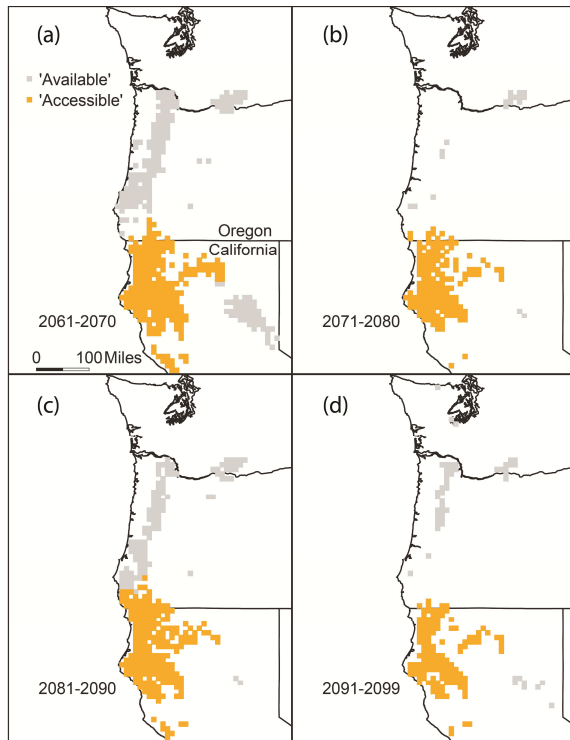
Figure 1. Range dynamics and the formation of a climate path "gap" for *Aneides*

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.
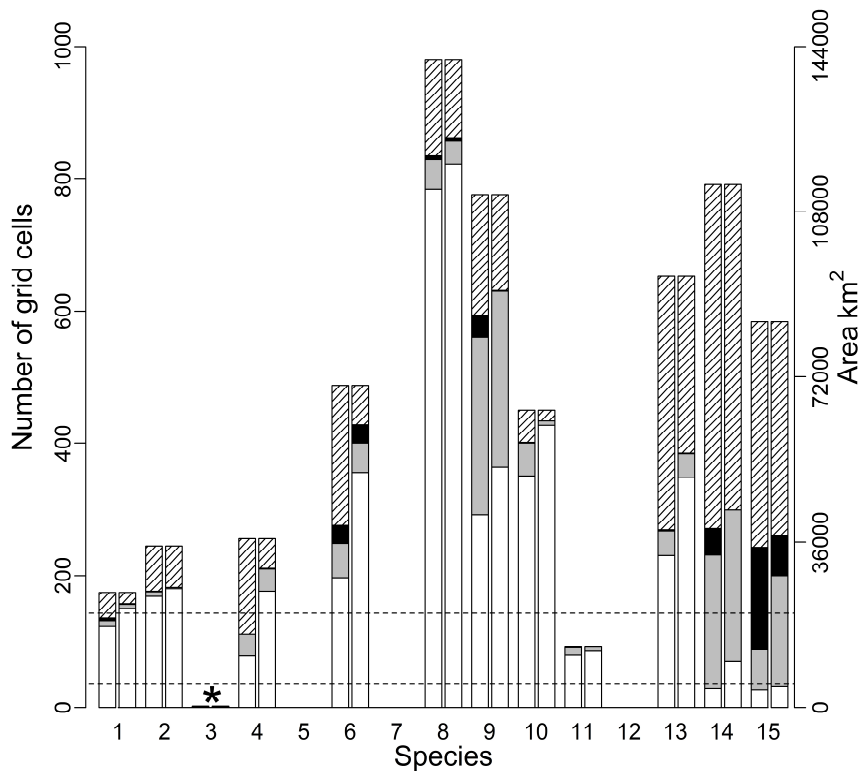
Figure 2. Mean predicted extent of occurrence (EOO) between 2071 and 2099 for

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

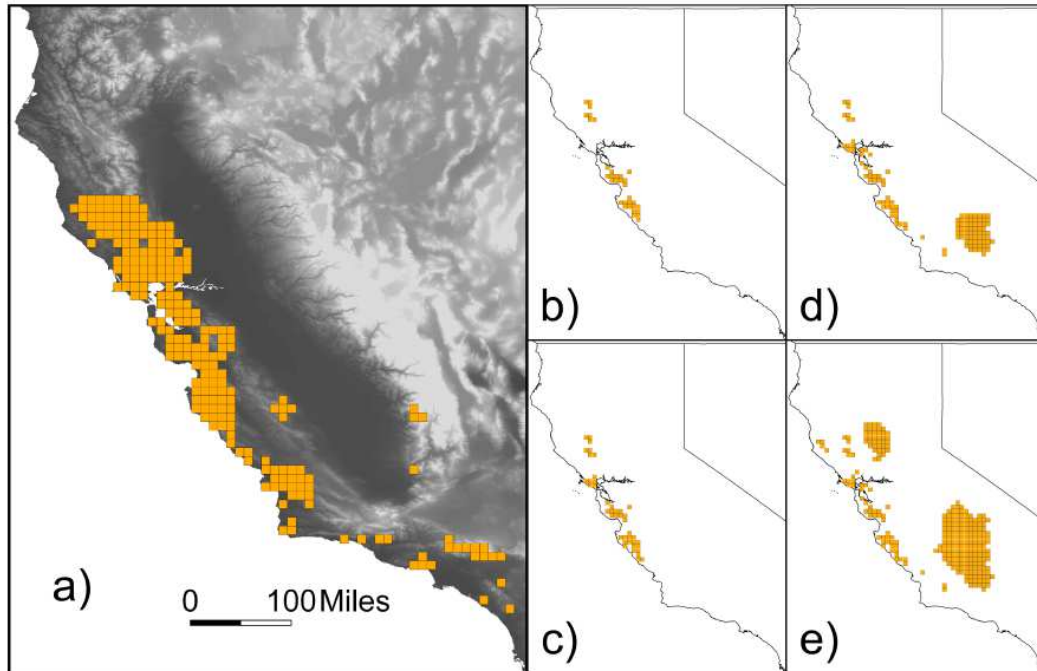predicted to have no suitable climate space under HCM B1.

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.
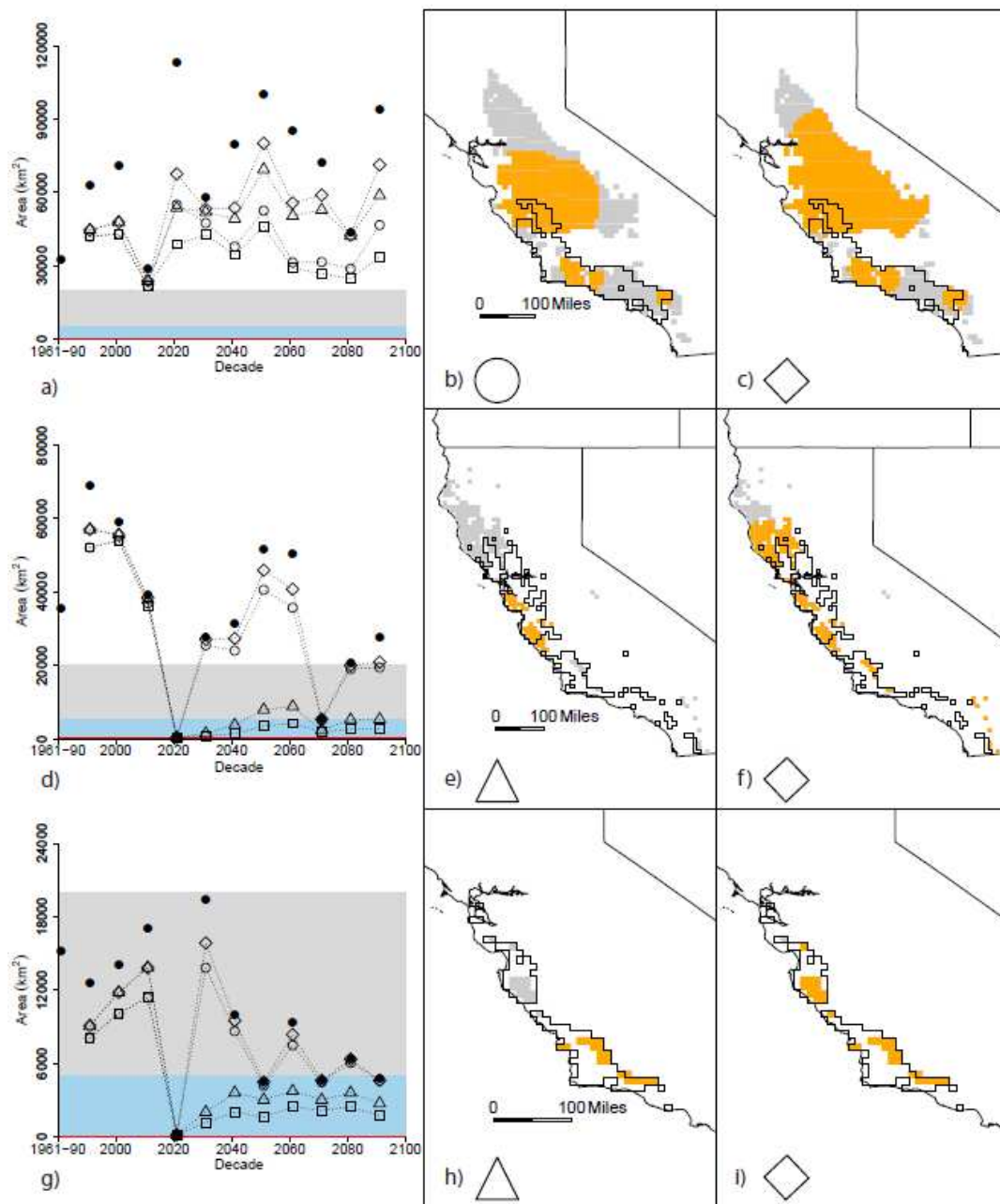
Figure 4. Range shift predictions for three species in California ((a-c) *Batrachoseps*

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

= 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.