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Projected Climate Impacts for the Amphibians of the Western Hemisphere

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Abstract: *Given their physiological requirements, limited dispersal abilities, and hydrologically sensitive habitats, amphibians are likely to be highly sensitive to future climatic changes. We used three approaches to map areas in the western hemisphere where amphibians are particularly likely to be affected by climate change. First, we used bioclimatic models to project potential climate-driven shifts in the distribution of 413 amphibian species based on 20 climate simulations for 2071–2100. We summarized these projections to produce estimates of species turnover. Second, we mapped the distribution of 1099 species with restricted geographic ranges. Finally, using the 20 future climate-change simulations, we mapped areas that were consistently projected to receive less seasonal precipitation in the coming century and thus were likely to have altered microclimates and local hydrologies. Species turnover was projected to be highest in the Andes Mountains and parts of Central America and Mexico, where, on average, turnover rates exceeded 60% under the lower of two emissions scenarios. Many of the restricted-range species not included in our range-shift analyses were concentrated in parts of the Andes and Central America and in Brazil's Atlantic Forest. Much of Central America, southwestern North America, and parts of South America were consistently projected to experience decreased precipitation by the end of the century. Combining the results of the three analyses highlighted several areas in which amphibians are likely to be significantly affected by climate change for multiple reasons. Portions of southern Central America were simultaneously projected to experience high species turnover, have many additional restricted-range species, and were consistently projected to receive less precipitation. Together, our three analyses form one potential assessment of the geographic vulnerability of amphibians to climate change and as such provide broad-scale guidance for directing conservation efforts.*

Keywords: amphibians, bioclimatic models, climate change, climate impacts, dispersal, range shifts, rare species, western hemisphere

Proyección de Impactos del Clima sobre los Anfibios del Hemisferio Occidental

Resumen: *Debido a sus requerimientos fisiológicos, sus habilidades de dispersión limitadas y los hábitats hidrológicamente sensibles, es muy probable que los anfibios sean muy sensibles a los cambios climáticos en el futuro. Utilizamos tres métodos para elaborar mapas de áreas en el hemisferio occidental donde es particularmente probable que los anfibios sean afectados por el cambio climático. Primero, utilizamos modelos bioclimáticos para proyectar cambios potenciales, impulsados por el clima, en la distribución de 413 especies de anfibios con base en 20 simulaciones del clima entre 2071 y 2100. Sintetizamos estas proyecciones para producir estimaciones de renovación de especies. Segundo, elaboramos mapas de la distribución de 1099 especies con distribución geográfica restringida. Finalmente, utilizando las 20 simulaciones de cambio climático en el futuro, elaboramos mapas que fueron proyectados consistentemente para recibir menos precipitación estacional en el próximo siglo y por lo tanto era probable que tuvieran microclimas e hidrologías locales alteradas. La renovación de especies proyectada fue mayor en los Andes y en partes de Centro América*

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y México, donde, en promedio, las tasas de renovación excedieron el 60% bajo el menor de dos escenarios de emisiones. Muchas de las especies de distribución restringida no incluidas en nuestros análisis de cambio de distribución se concentraron en partes de los Andes y de América Central y en el Bosque Atlántico de Brasil. La mayor parte de América Central, suroeste de América del Norte y partes de América del Sur consistentemente fueron proyectadas para experimentar disminución en la precipitación para fines de este siglo. La combinación de los resultados de los tres análisis resaltó varias áreas en las que es probable que los anfibios sean afectados significativamente por el cambio climático por múltiples razones. Algunas porciones del sur de América Central fueron proyectadas simultáneamente para experimentar una tasa de renovación alta, incluir muchas especies de distribución restringida adicionales y fueron proyectadas consistentemente para recibir menos precipitación. En conjunto, nuestros tres análisis constituyen una evaluación potencial de la vulnerabilidad geográfica de los anfibios al cambio climático y como tal proporciona directrices a gran escala para la orientación de los esfuerzos de conservación.

Palabras Clave: anfibios, cambio climático, cambios de distribución, dispersión, especies raras, hemisferio occidental, impactos climáticos, modelos bioclimáticos

Introduction

Globally, more than 32% of amphibian species are listed as vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature (IUCN) and some estimates suggest 122 species have gone extinct since 1980 (Stuart et al. 2004; Mendelson et al. 2006; Wake & Vrendenburg 2008). These population declines have been attributed to a number of factors, including habitat loss, disease, and climate change (Collins & Storfer 2003). Habitat loss is generally considered the most important cause of amphibian population declines (Cushman 2006), although disease has been linked to some declines, mainly in tropical regions (Daszak et al. 2003). Nonetheless, it is likely that for many populations, multiple interacting threats are responsible for declines (Blaustein & Kiesecker 2002).

Amphibians are likely to be highly sensitive to climate change (Blaustein et al. 2003; Carey & Alexander 2003) for several reasons. Climatic shifts toward warmer, drier regimes are expected to have large effects on amphibians due to the physiological constraints associated with their highly water-permeable skin and ectothermic life history (Blaustein et al. 1994). Because survival and reproduction in most species require moist microclimates, water is a crucial resource for amphibians (Feder & Berggen 1992). Amphibian activity and migration are frequently positively correlated with precipitation (Gibbons & Bennett 1974). As in other ectothermic animals, temperature can influence multiple biological functions in amphibians, including energy acquisition and enzyme kinetics (Feder & Berggen 1992). These functions generally have thermal optima, with the rate of activity decreasing on either side of the optimum (e.g., Moore 1939; Freed 1980). Amphibians use behavioral and physiological mechanisms for thermoregulation, but these mechanisms are limited by the potentially conflicting demand for water economy (Hutchison & Dupré 1992).

Freshwater ecosystems, which are generally a key component of amphibian habitat, are among those systems most at risk due to climate change (IPCC 2007). Climate change is generally expected to result in higher surface water temperatures globally and more variable and intense precipitation and more days between precipitation events for some regions. These potential changes may affect stream flows, lake depths, the amount and duration of winter snow packs, pond hydroperiods, and soil moisture. Changes to the hydrological regime of amphibian habitats may negatively affect breeding success and survival. In addition, because dry, open areas can present barriers for migration, climate change has the potential to fragment amphibian habitat and thus hinder dispersal (Dodd & Smith 2003). At the same time, future climatic changes may increase suitable habitat for some species. For example, warmer temperatures may allow species that are currently limited by cold temperatures to expand poleward and upward in elevation.

Evidence for the large direct effects of climate change on amphibian populations is mounting. There is a correlation between years of extreme drought and population declines (e.g., Pounds & Crump 1994). Temperature changes have been correlated with population declines (Heyer et al. 1988), which suggests that environmental changes associated with climate change are likely to affect amphibian populations. Results of one recent study suggest that dramatic population declines of amphibians in Queensland, Australia, coincided with regional warming (Alford et al. 2007). Warming climates also directly affect breeding phenology and result in some amphibian populations breeding earlier (Beebee 1995; Blaustein et al. 2001; Chadwick et al. 2006).

Climate change has also been implicated as stimulating the emergence of infectious diseases at both local and global scales (Kiesecker et al. 2001; Pounds et al. 2006; Bosch et al. 2007). These diseases may affect amphibians at the population level. Unfortunately the relationships between global climate change and disease emergence are complex and difficult to understand (Lips et al. 2008).

Although recent climatic changes have been linked to changes in amphibian populations and phenologies,

only a few researchers have attempted to project potential future impacts of climate change on amphibians (e.g., Thomas et al. 2004; Araújo et al. 2006). Generally, these studies have relied on bioclimatic models to predict changes in species distributions. Most bioclimatic models are based on correlative relationships between the current distribution of a species and current climatic conditions. The models are then applied to projected future climate data to produce projections of future potential geographic ranges (Pearson & Dawson 2003). These correlative models are currently one of the best methods available for projecting potential continental-scale responses of many species to climate change.

Although useful, correlative bioclimatic models have several limitations (Pearson & Dawson 2003). First, bioclimatic models do not take evolutionary processes into account. Although it is unlikely that many species will be able to adapt to the projected rapid changes in climate, it is possible that some species will be able to evolve relatively quickly (Skelly et al. 2007). If species can adapt to rapidly changing conditions, bioclimatic models will overestimate potential range shifts. Second, correlative bioclimatic models generally do not directly address biotic interactions. These models can only capture predator–prey, competitor, or certain habitat relationships indirectly through correlative associations with climate. Climate-driven changes to these correlative associations can result in the introduction of additional error into model projections. By failing to directly account for biotic interactions, bioclimatic models may underestimate the impacts of climate change in some cases and overestimate it in others. A related limitation of correlative bioclimatic models involves the data with which the models are built. Because these models are almost always based on the current distribution of a species—in essence, the realized niche—they may not capture all of the climatic conditions under which a species can exist. Thus, the models will be less accurate for species that have been extirpated from much of their historic range due to hunting, land-use change, or other nonclimatic forces.

Finally, errors in bioclimatic models can result in large uncertainties in projections of potential future ranges. Applying different bioclimatic modeling approaches to the same data can result in large discrepancies in projected future potential ranges (Lawler et al. 2006; Pearson et al. 2006). Ensemble modeling approaches that reduce these model uncertainties may be a solution to this problem (Araújo & New 2007). Despite the limitations of bioclimatic models, they are powerful tools that provide a first approximation of how species might respond to climate change at broad scales. They cannot necessarily accurately predict the future location of a given species. They can, however, provide estimates of the likely relative magnitude of the impacts of climate change on species distributions in different areas.

We augmented a set of bioclimatic model projections with two other analyses to assess geographic variation in amphibian vulnerability (defined here as decreased viability of individuals and populations) to climate change in the western hemisphere. The bioclimatic model projections provide a general indication of where changes in amphibian faunas might be expected to be greater and lesser. We supplemented these projections by mapping the cumulative distributions of 1099 restricted-range species that could not be accurately modeled with bioclimatic models. If these species' limited ranges reflect specific physiological or habitat requirements, they may be more susceptible to climate change. Finally, we mapped areas that were consistently projected to get warmer and receive less seasonal precipitation in the coming century. These climatic changes will likely affect microclimates and local hydrologies and thus may adversely affect sensitive amphibian habitats. We combined the results of the three assessments to identify areas in the western hemisphere where climate change may have large impacts on amphibian populations.

Methods

Data

We derived modern climate data from the University of East Anglia Climatic Research Unit (CRU) CL 1.0 (New et al. 1999), CL 2.0 (New et al. 2002), and TS 2.1 (Mitchell & Jones 2005) climate data sets. We applied these data to a 50 × 50 km resolution grid of the western hemisphere with a locally weighted, lapse-rate-adjusted interpolation method developed by P. J. Bartlein (personal communication) to create monthly data for the period of 1901–2002. We averaged the monthly data from this time series to produce a 1961–1990 30-year mean modern climate baseline.

We created future climate data from coupled atmosphere–ocean general circulation model (AOGCM) simulations in the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multimodel data set. For each of 10 AOGCMs (see Supporting Information), we used 2001–2100 monthly data simulated under the Special Report on Emissions Scenarios (SRES) B1 (low) and A2 (mid-high) greenhouse-gas emissions scenarios (Nakicenovic et al. 2000). These scenarios produce estimated global mean temperature increases of 2 °C (B1) and 3–4 °C (A2) by the end of the century (IPCC 2007). We calculated anomalies between each month of the simulated 2001–2100 climate data and a 1961–1990 30-year monthly mean created from the AOGCM 20th century simulation. We interpolated these anomalies to the 50 × 50 km grid with a bilinear distance-weighted method and applied the interpolated anomalies to the downscaled CRU 1961–1990

30-year mean climate data to create monthly future climate data.

We calculated 37 bioclimatic variables from both the CRU and monthly future climate data with an approach modified from Cramer and Prentice (1988) and soil data from the Global Soil Data Task (2000) (Lawler et al. 2009). Several of these variables, including temperature and moisture indices that were based on actual and potential evapotranspiration, likely directly influence amphibian distributions at large spatial scales. Other variables such as growing-degree days may serve as surrogates for vegetation that may influence the distribution of some amphibians.

We used digital range maps for 1616 amphibian species to represent species distributions in our models (IUCN et al. 2004). These range maps were sampled with the same 50-km grid used to summarize the climate data. We used a 50-km grid to balance the inaccuracies associated with mapping fine-scale environmental conditions at coarser resolutions and mapping relatively coarse resolution range-map data at finer resolutions. In general, range maps overestimate species' occurrences (Hurlbert & White 2005); however, for many rare amphibians, distribution data are limited and ranges are relatively poorly defined. Thus, for many of the rarer species in our data set, the range maps we used are likely to underestimate species distributions (IUCN et al. 2004).

Range-Shift Projections

The bioclimatic models we used were developed by Lawler et al. (2009) who employed random forest predictors (Breiman 2001) to project potential range shifts. Random forests are a model-averaging approach derived from regression trees, or as in our study, classification trees. Random forests are a flexible modeling tool for ecological problems in general (Cutler et al. 2007) and are relatively accurate compared with other modeling approaches (Lawler et al. 2006; Peters et al. 2007). Bioclimatic models predict the suitable environmental conditions for a species. When projected future climate data are used as inputs to the models, they predict where environmental conditions may be suitable in the future. Here we refer to projected shifts in the areas that contain suitable environmental conditions as potential range shifts.

We built the models with 80% of the range data (80% of the presences and 80% of the absences) for each species and set the remaining 20% of the data aside for model evaluation. We built models for 1616 species, but selected only those species with models that predicted at least 90% of the test-set presences and at least 80% of the test-set absences correctly. This screening process left 413 species for use in our range-shift analyses (Supporting Information). Future potential ranges for each of these 413 species were projected with the simulated 2071–2100 30-year mean bioclimatic data as the predictor variables in each species' model. For the most part, the species we were unable to model were those with smaller ranges. The average range size of the species included in the range-shift analyses was approximately 195,5000 km^2, and the average range size of those species not included was 82500 km^2. At least some of the excluded species that had larger ranges also tended to have more fragmented ranges, and a few were mountainous species.

We summarized the potential range shifts across all species by calculating species turnover in each grid cell. Turnover was calculated as the number of species projected to experience a contraction of their potential range in a cell plus the number of species projected to experience an expansion of their potential range into that cell divided by the total number of species currently in the cell. We summarized the turnover values for the 10 projections made with the lower (B1) and higher (A2) emissions scenarios by calculating the 20th percentiles of the distributions of turnover values. The 20th percentile is a relatively conservative estimate of change—eight of the 10 future climate projections resulted in turnover rates of at least the amount of change represented by the 20th percentile. We further summarized these changes by ecoregion. We used ecoregion classifications for South and Central America (Griffith et al. 1998) and North America (Commission for Environmental Cooperation 1997) to summarize our results for 79 different ecoregions in the western hemisphere. For each ecoregion, we calculated the mean of the 20th percentile values for all cells in the ecoregion, which produced an estimate of the average cell-by-cell turnover across the ecoregion. This is the amount of turnover one might expect, on average, at any one point in the ecoregion. It does not imply absolute species losses or gains across the ecoregion as a whole.

In addition to calculating turnover, we summarized projected losses in the area of the potential ranges of each of the 413 species. Range loss was calculated by taking the difference in the size of the current range and the projected future range of a species and dividing by the size of the current range. Range-loss calculations were made for 10 different future range projections for each species on the basis of 10 different climate projections. The range-loss values we report represent the 20th percentile of the 10 values.

We assessed the effects of dispersal limitations on potential range changes by restricting any potential future range expansions to 200, 100, and 50 km. Approximately 70% of surveyed amphibian species have a maximum annual dispersal distance of $\leq$1 km, whereas 44% have a maximum annual dispersal distance of $\leq$400 m (Smith & Green 2005). Five percent of surveyed amphibian species, mostly anurans (frogs and toads), have a maximum annual dispersal distance of $\geq$10 km (Smith & Green 2005). Thus, a small minority of species may be able to disperse up to 200 km over a 100-year period. Many species,

however, may be limited to an area within 50 km of their current range. For each species, we calculated projected range losses, range expansions, and net changes in potential range size under the assumptions of no dispersal limitation and the three dispersal limitation distances. We then calculated the average projected changes for all 413 species and the average changes for anurans, caudates (salamanders), and gymnophonia (caecilians).

Restricted-Range Species

Species with restricted geographic ranges are likely to be relatively sensitive to changes in climate. We defined restricted-range species as those occupying fewer than 100 50-km grid cells, an area roughly the size of Ecuador or the U.S. state of Wyoming. These species often have specific habitat requirements that are generated by unique combinations of physical and biological factors. There is evidence that many of these isolated, unique environments may disappear in coming decades (Saxon et al. 2005).

In addition to being relatively sensitive to climatic changes, species with small ranges are also difficult to model with correlative modeling approaches. Many of the species for which we were unable to build accurate models had small or fragmented ranges. Because we conducted our range-shift analyses with only those species for which we were able to build relatively accurate models, the results of those analyses likely underestimate range shifts in areas with more restricted-range species. Of the 1616 species in our data set, 1187 had ranges that occupied fewer than 100 grid cells. Of these 1187 species, 1099 were not included in our range-shift analyses. We tallied the number of these 1099 unmodeled species in each of the 79 ecoregions and mapped the tallies. These estimates of the number of restricted-range species in each ecoregion were a second, complementary assessment of areas likely to experience large changes in amphibian fauna.

Precipitation Patterns

Changes in precipitation can have direct effects on particular microclimates and habitats used by amphibians. Although our range-shift projections likely captured some of these effects—particularly in terms of broad-scale physiological constraints—they undoubtedly failed to capture potential changes in hydrology and in microclimates that could make areas more or less hospitable for certain species. We assessed potential changes in sensitive amphibian habitats and microclimates by identifying areas that were consistently projected to experience at least a 10% decrease in precipitation during at least one season of the year. For both the lower and higher emissions scenarios, we calculated the proportion of the 10 climate-change projections that simulated a decrease in seasonal precipitation for the 2071–2100 30-year mean period relative to the base period of 1961–1990. Seasons were defined as December–February, March–May, June–August, and September–November. We then calculated the percentage of grid cells in each ecoregion for which at least eight of the 10 climate projections resulted in at least a 10% decrease in precipitation.

Geographic Vulnerability to Climate Change

We assessed the relative vulnerability of amphibians to climate change by mapping ecoregions that, on average, were projected to have at least 50% turnover, at least 50 restricted-range species, and precipitation decreases of at least 10% in at least 20% of the grid cells. We then labeled each of the ecoregions as meeting zero, one, two, or three of these criteria for indicating vulnerability. These thresholds are arbitrary and thus produce only one potential map of climate vulnerability. Other combinations of thresholds would produce different maps, although the general patterns of vulnerability are likely to be similar.

Results

Range-Shift Projections

Species showed a wide range of responses to projected future climatic changes (Fig. 1). Several species (e.g., the northern leopard frog [*Rana pipiens*]) were projected to experience poleward or elevational shifts in their ranges (Fig. 1). Other species (e.g., the yellow-banded poison dart frog [*Dendrobates leucomelas*]) had projected range changes that were more spatially complex (Fig. 1). Overall, species were projected to experience larger range contractions than range expansions (Table 1). There was little difference in the sizes of range contractions and expansions across the three amphibian orders. Average range expansions, even assuming unlimited dispersal, were relatively modest. Nevertheless, the variation in range expansions assuming unlimited dispersal was large, ranging from 0% to 635% under the lower emission scenario and from 0% to 1200% under the higher emissions scenario.

Limiting dispersal resulted in relatively little change in the overall pattern of range contractions (Fig. 2). Eighty-five percent of all species were projected to experience a net loss in total range area under the lower emissions scenario when no dispersal limitations were applied. When dispersal was limited to an area within 50 km of the current range, 95% of species were projected to experience a net loss in range size under the lower emissions scenario (Fig. 2a). Differences in the percentage of species projected to lose all their current range given the limited and unlimited dispersal scenarios were even smaller. For example, under the lower emission scenario, 13% of all species were projected to lose 100% of their current range when dispersal was assumed to be unlimited and

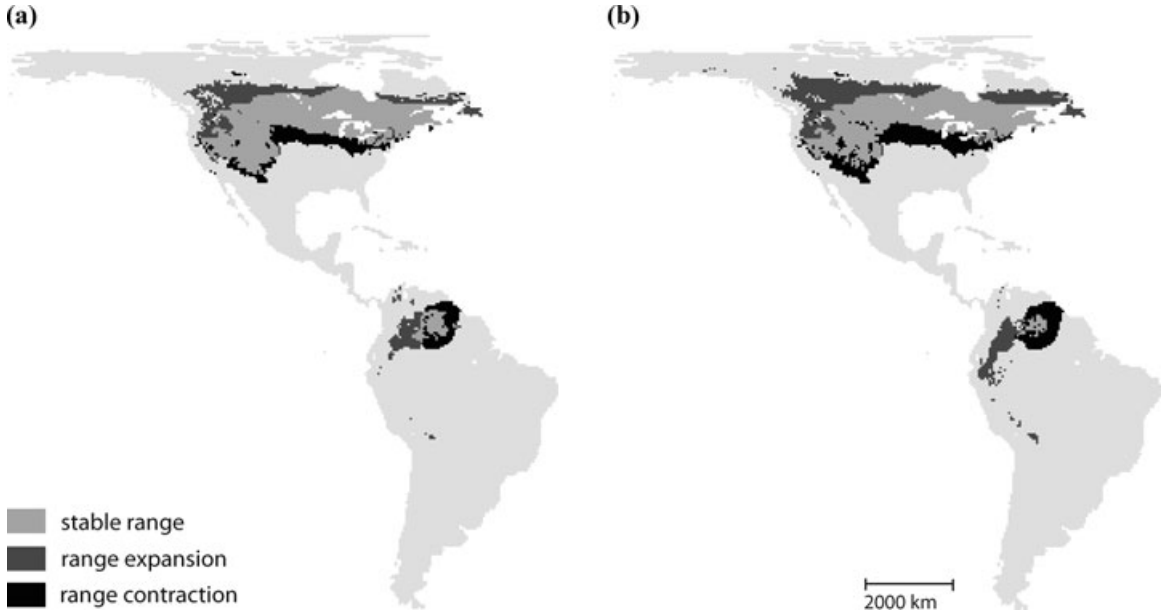

*Figure 1. Projected changes in the potential ranges of the northern leopard frog (*Rana pipiens*) (North America) and the yellow-banded poison dart frog (*Dendrobates leucomelas*) (South America) in response to climatic changes as projected by the UKMO-HadCM3 general circulation model run for a (a) lower and (b) higher greenhouse-gas emissions scenario for the years 2071–2100.*

15% were projected to lose 100% of their current range when dispersal was limited to 50 km.

Much of the western hemisphere was projected to experience relatively large changes in amphibian faunas (Fig. 3). Under the lower emissions scenario, most ecoregions were, on average, projected to experience at least 10% turnover, and many were projected to experience at least 20% turnover. The Yungas (part of the central Andes Mountains) and the Northern Andes Highlands ecoregions were projected to experience some of the highest turnover, on average 465% and 161%, respectively. Turnover rates exceeded 100% in areas projected to experience a large number of range expansions relative to the number of species currently present. The ecoregions themselves were not projected to experience those changes, but rather on average, for any given grid cell in an ecoregion, eight of the 10 climate-change projections resulted in at least that much turnover. Under the higher emissions scenario, most ecoregions were, on average, projected to experience at least 30% turnover in amphibian species with many ecoregions in western South America, Central America, and the eastern United States projected to experience at least 50% turnover. The relatively high rates of turnover projected for the tundra

Table 1. Projected climate-induced range contractions and expansions (as percentage of observed range) of 413 amphibian species for two different greenhouse-gas emissions scenarios and four different dispersal scenarios.[a]

*Taxon (*n*)*	*Contraction*	*Expansion (unlimited dispersal)[b]*	*Expansion (200-km limit)[b]*	*Expansion (100-km limit)[b]*	*Expansion (50-km limit)[b]*
Low emissions (B1 scenario)					
Anura (360)	39 (29)	11 (35)	7 (10)	6 (5)	4 (5)
Caudate (45)	39 (30)	17 (18)	15 (14)	12 (11)	8 (8)
Gymnophonia (8)	27 (27)	12 (18)	7 (9)	4 (2)	1 (2)
all amphibians (413)	39 (29)	12 (33)	8 (10)	6 (8)	4 (5)
Mid-high emissions (A2 scenario)					
Anura (360)	51 (31)	15 (66)	8 (13)	5 (5)	3 (5)
Caudate (45)	53 (29)	21 (50)	13 (17)	8 (11)	5 (8)
Gymnophonia (8)	41 (31)	16 (25)	7 (10)	4 (1)	1 (1)
all amphibians (413)	51 (31)	16 (64)	8 (13)	6 (8)	3 (5)

[a] *Values are means (SD) of the 20th percentiles of distributions of the 10 projected range changes for each species simulated with climate projections from each of 10 coupled atmosphere-ocean general circulation models (AOGCMs). The 10 projected values correspond to climate projections from 10 different AOGCMs. All values are percentages.*
[b] *Species were allowed to fully occupy projected future ranges (unlimited dispersal) and occupy portions of that projected future range (in parentheses).*

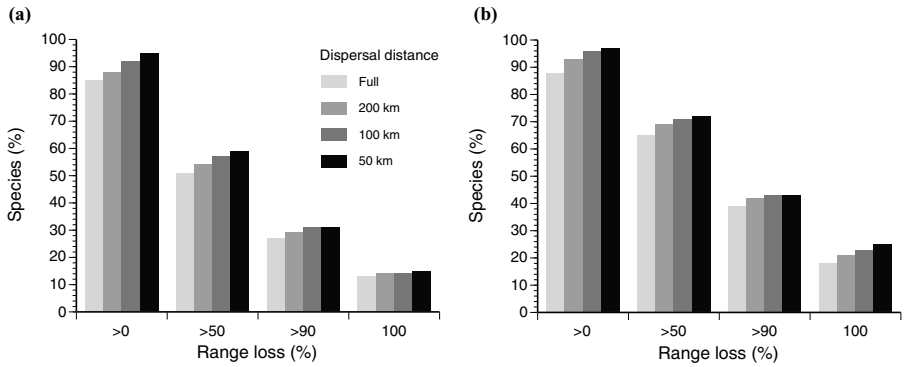

Figure 2. The percentage of 413 amphibian species projected to experience four different levels of range loss in response to climate change given four different assumptions about dispersal limitations for both a (a) lower and (b) higher greenhouse-gas emissions scenario.

along the northern and western coasts of Alaska, parts of the taiga (under the higher emissions scenario), and the Caribbean islands were in part an artifact of having relatively few modeled species in these areas. In each of these areas, there were on average fewer than five modeled species. Thus, small changes in species numbers in those ecoregions resulted in high turnover rates.

Restricted-Range Species

The largest concentrations of the restricted-range species not included in our range-shift analyses were in ecoregions of Central and South America: Northern Andes ecoregion (239 species), Atlantic Forests (199 species), Caribe-Pacific Lowland Plains and Hills (northern end of the Andes; 142 species), and Central American Isthmus (164 species) (Fig. 4a). As expected, the distribution of restricted-range species closely reflected the pattern of species richness in general (Fig. 4b).

Precipitation Patterns

There were several ecoregions that were consistently projected to experience decreases in precipitation in at least one season under both the lower and higher emission scenarios (Fig. 5). Much of Mexico and Central America and a number of ecoregions in South America, including the Caatinga (in northeastern Brazil), Peruvian and Atacaman Deserts, and Valdivian Forested Hills and Mountains (in the southern Andes), were most consistently projected to experience drying. Under the higher emission scenario, additional areas in western North America and southern South America had projected decreases in precipitation.

Geographic Vulnerability to Climate Change

Amphibians in several areas in Central and western South America are likely to be highly vulnerable to future projected climatic changes (Fig. 6). Under the lower

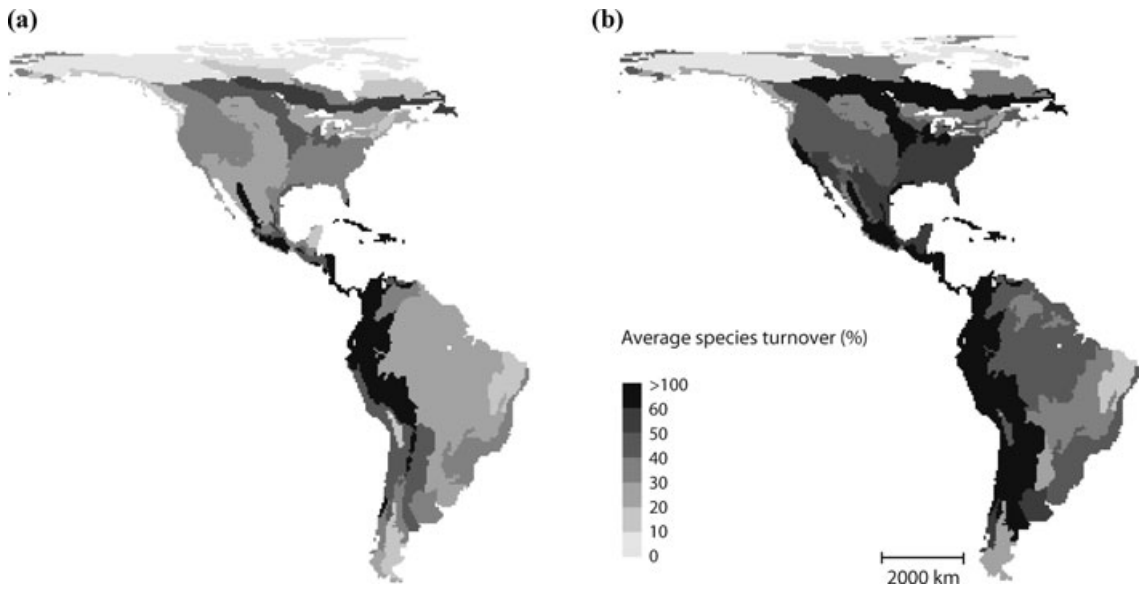

Figure 3. Projected climate-induced turnover in amphibian fauna across the western hemisphere under (a) lower and (b) higher greenhouse-gas emissions scenarios for the years 2071–2100. Values are average turnover across each ecoregion.

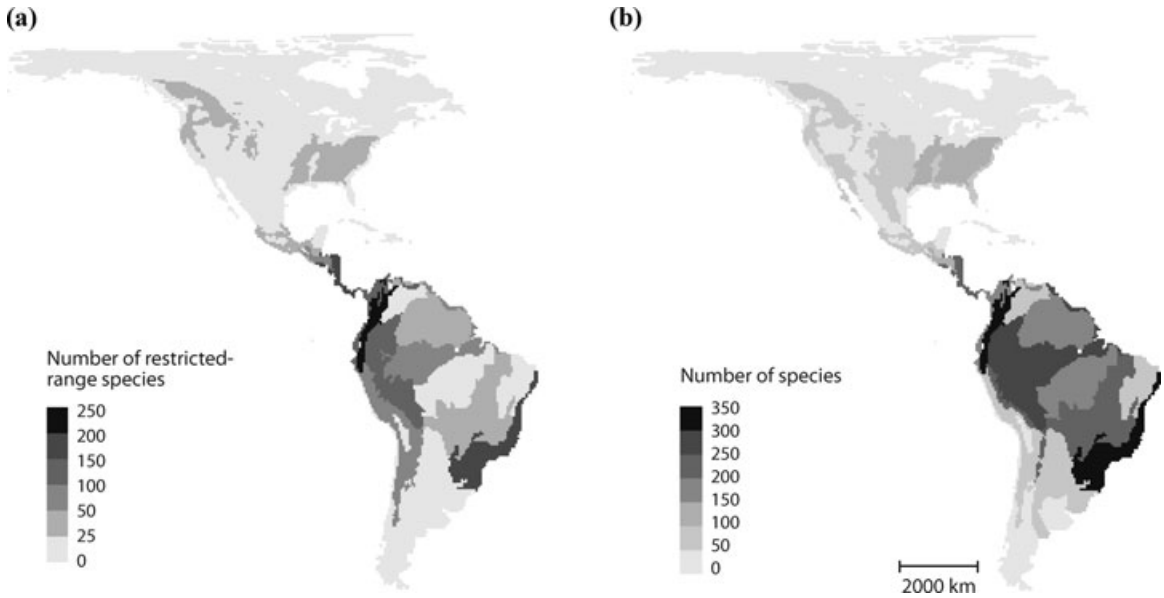

Figure 4. The number of (a) restricted-range amphibian species (n = 1099) and (b) all amphibian species (n = 1616) by ecoregion in the western hemisphere. A species was considered range restricted if it occurred in <100,50 × 50 km grid cells in the western hemisphere. Only the restricted-range species not included in our range-shift analyses are mapped.

emissions scenario, the Central American Isthmus ecoregion was simultaneously projected to have high species turnover, contained a high concentration of restricted-range species, and was consistently projected to receive less precipitation in at least one season at the end of the century. Several neighboring ecoregions, including the Northern Central American Highlands and portions of the Northern Andes, were also projected to have high values for all three indicators given climate projections derived from the higher emissions scenario. Other ecoregions were vulnerable to climate change in at least two of the three ways. For example, the Western Sierra Madre, the northern Andes, and the western Amazon Basin (Amazon Irregular Plains and Piedmont ecoregion) were projected to have high values for two of the three indicators under the lower emissions scenario. Under the

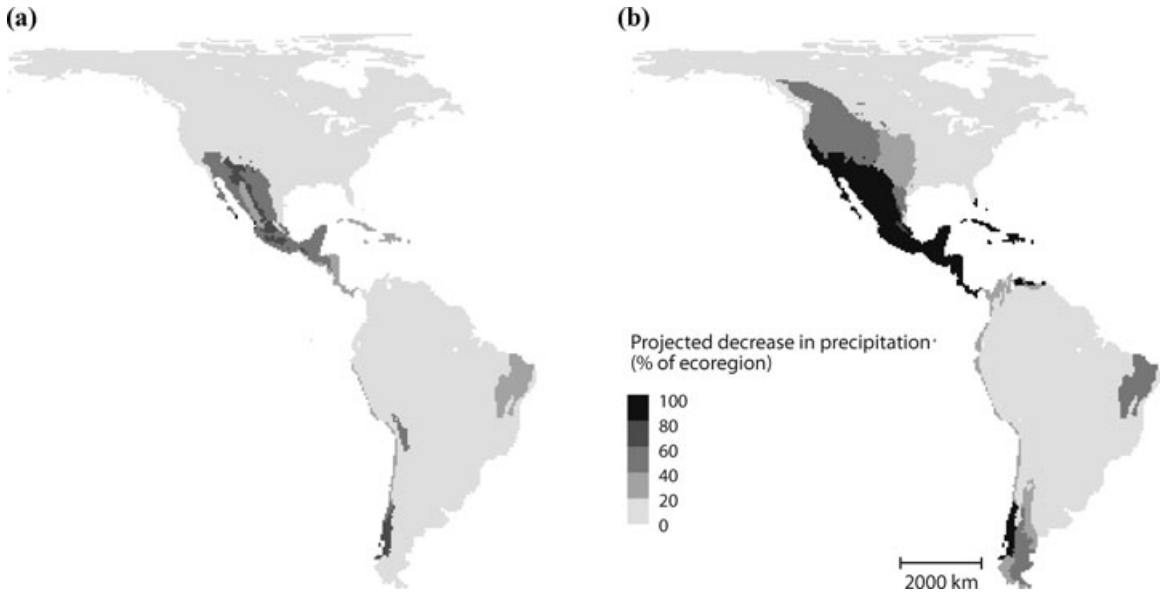

Figure 5. Projected seasonal decreases in precipitation for years 2071–2100. The values in the maps represent the percentage of an ecoregion for which at least 8 of 10 climate-change projections resulted in at least a 10% decrease in precipitation in any of four seasons for a (a) lower and (b) higher greenhouse-gas emissions scenario.

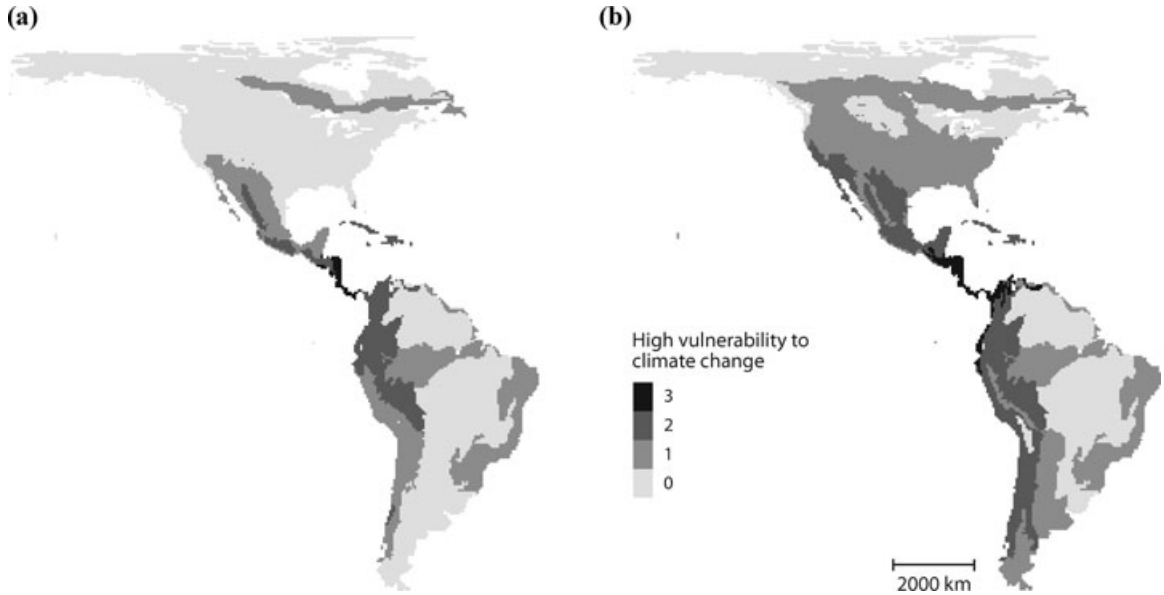

Figure 6. Maps of the potential vulnerability of amphibian faunas to climate change on the basis of three separate indices generated for a (a) lower and (b) higher greenhouse-gas emissions scenario. Ecoregions received a score of zero to three, depending on the number of indices for which they were ranked highly vulnerable. Highly vulnerable ecoregions are those projected to have at least 50% turnover, that had at least 50 restricted-range species, or in which at least 20% of the 50 × 50 km grid cells were consistently projected to experience decreases in precipitation of at least 10% in any one season. The shading on the maps corresponds to the number of these three criteria that were met in each ecoregion.

higher emissions scenario, North American warm deserts, Mediterranean California, and portions of the central and southern Andes had high projected values for two indicators.

Some ecoregions that were projected to have relatively little species turnover had large concentrations of restricted-range species or were consistently projected to experience decreases in precipitation in at least one season at the end of the century. For example, under the higher greenhouse-gas emissions scenario, the Caatinga ecoregion in northeastern Brazil was, on average, projected to experience 13% turnover and contained only 11 restricted-range species. Nonetheless, 57% of the ecoregion was consistently projected to experience seasonal precipitation decreases. Similarly, although the Atlantic Forests ecoregion along the Atlantic coast of South America was not projected to experience the highest amounts of species turnover or the most consistent decreases in precipitation, it is home to some of the most restricted-range species in the hemisphere and thus is likely to be an area in which amphibian faunas will be more vulnerable to climatic changes.

Discussion

Our results demonstrate the potential for major shifts in amphibian faunas over the coming century. More importantly, the three complementary assessments of potential vulnerability to climate change highlight several areas that are projected to experience large climate-driven changes. Areas of high projected turnover of species, areas rich in restricted-range species, and areas consistently projected to experience reductions in seasonal precipitation will likely be sites of some of the largest changes in amphibian fauna.

The high projected turnover in amphibian faunas in much of the Andes, Central America, and portions of the boreal forest is likely the result of a combination of factors. First, some of these areas are projected to experience relatively large climatic changes. For example, high northern latitudes are projected to experience the most warming, and Central America and Mexico are consistently projected to experience changes in precipitation. The projected climatic changes alone, however, do a poor job of explaining the patterns of high projected species turnover. A second factor that likely explains these patterns is the distribution of species' range boundaries. Areas with a high density of range edges are more likely to experience high turnover than areas with relatively few species' range boundaries. Mountainous regions have strong environmental gradients and consequently are likely to be the site of many range movements. Other regions, such as the Softwoods Shield Northern Forests ecoregion, which stretches across much of North America between 50° and 60° north latitude, are at the

northern or southern boundary of many species current ranges and are consequently likely to also be sites of significant faunal change.

In areas of high turnover, dispersal abilities and landscape connectivity will affect a species' ability to track climate change. Dispersal abilities vary among the three amphibian orders. Although little is known about dispersal in caecilians, anurans may be able to disperse further on average than caudates (Smith & Green 2005). Even assuming unlimited dispersal, however, our potential range-shift projections indicated that many species would likely experience significant overall range contractions, largely because range contractions (i.e., the loss of suitable climates) were larger than range expansions (i.e., projected new suitable climates) and thus were driving the net changes in potential range size. Nevertheless, our models did project large range expansions for some species. For example, the potential future ranges of the western narrow-mouthed toad (*Gastrophryne olivacea*), the coastal plain toad (*Bufo nebulifer*), and the emerald-eyed tree frog (*Hyla crepitans*) were projected to be 64%, 51%, and 74% larger, respectively, than their current ranges. In addition, for some species, our models likely overestimated range contractions and underestimated range expansions. For example, as climate changes, new climatic conditions may be created that are suitable for a particular species but that have no current analogues. Given the correlative nature of the bioclimatic models, our results may classify these climates as unsuitable because the species does not currently exist under these climates. Furthermore, many of the species for which we were unable to build accurate models had very small or fragmented ranges. It is these species for which dispersal abilities and landscape connectivity will be most critical.

For those species for which range contractions are likely to be larger than range expansions, early management activities focused on preserving populations in areas that are projected to experience less change may be more effective than planning for translocations into new areas. Conversely, for species projected to experience both large range contractions and large range expansions, and for many species with small ranges, successful management may require creating new habitats in areas that become more suitable and moving individuals into those areas. For those species with highly limited dispersal capabilities, translocations may prove to be critical. Thus, ecologists, managers, and policy makers will all need to grapple with the difficult ecological and philosophical issues surrounding translocations (Hunter 2007; McLachlan et al. 2007).

The cumulative results of our three vulnerability assessments provide a convincing argument for augmenting range-shift analyses with other complementary evaluations. For example, although the Caatinga ecoregion in northeastern Brazil was projected to experience relatively little species turnover and has relatively few restricted-range species, it was one of the ecoregions most consistently projected to experience less seasonal precipitation in the coming century. Thus, microclimates and hydrology in parts of the Caatinga might change in ways that significantly affect amphibian populations.

Although we investigated three ways in which amphibians might be sensitive to climate change, we did not address all sensitivities. Climate change may indirectly affect amphibians through the facilitation of disease spread and infection. The expansion of a pathogen into new regions with naïve hosts can result in catastrophic mortality events (Tompkins et al. 2003; Wikelski et al. 2004). For example, in the New World tropics, temperatures in higher-elevation sites appear to be shifting toward the growth optimum for an important amphibian pathogen, *Batrachochytrium dendrobatidis*, that may contribute to population declines of several amphibian species (Pounds et al. 2006; Seimon et al. 2007). Moreover, rising temperatures have been linked to *Batrachochytrium* outbreaks in Spain (Bosch et al. 2007). Climate change may also facilitate infection by reducing the immune response of amphibian hosts. For example, altered hydrological regimes due to climate change may lead to rapid pond drying. Wood frog (*Rana sylvatica*) juveniles exposed to rapid pond drying as tadpoles exhibit reduced immune function, suggesting that alterations in hydroperiod could lead to increased infectivity in hosts (Gervasi & Foufopoulos 2008). Climate change and pathogens can also interact with other environmental stressors to increase susceptibility of hosts to pathogens (Kiesecker et al. 2001). Likewise, climate change may result in the movement of predators, prey, or competitors, thus further altering the suitability of a given site for a given species.

Although the effects of climate change are likely to be widespread and significant, habitat loss due to human land use will continue to play a large role in population declines and species extinctions (Jetz et al. 2007). Future land-use change, particularly in the tropics, may significantly reduce the amount of available habitat for many species and exacerbate climate-change impacts on species by making dispersal to suitable habitat more difficult. Given these and other potential threats, it is important to view our geographic assessment of amphibian vulnerability as just one of several possible broad-scale assessments.

There were distinct limits to the species-range maps used to build our models (IUCN et al. 2004). In general, these limitations likely had little effect on our results. Overestimation of the current distribution of species likely resulted in overestimates of the future range of species. Although this might have slightly affected spatial accuracy of our turnover estimates in 50 × 50 km cells, it did not likely affect turnover patterns as summarized at the scale of ecoregions or the magnitude of turnover in a consistent way. Underestimation of the distribution

of species with smaller ranges, and particularly those in more remote locations, may have caused us to underestimate the number of restricted-range species in general and in the tropics in particular. Again, however, because we summarized the 50-km results by much larger ecoregions, the general patterns of restricted-range species distributions are likely to be relatively accurate.

Although our approach of using only relatively accurate bioclimatic models in our analyses reduced the amount of uncertainty in our range-shift projections, these projections still involve a significant degree of uncertainty. Some of that uncertainty comes from inaccuracies in maps of current species distributions. For some species, however, future range shifts will be driven by complex interactions among multiple species or by specific biotic interactions that are poorly captured by simple correlative models involving climate. Nonetheless, many animal species have shifted their ranges in response to recent climatic changes in relatively simple and predictable ways (Parmesan 2006). Shifts in the distributions of many species have occurred in directions and at rates that directly reflect recent changes in temperature (Parmesan & Yohe 2003; Root et al. 2003). Thus, the types of range shifts projected by our models are likely to be reasonable for many species.

There are also caveats that accompany our precipitation analysis. Whether a precipitation decrease is ecologically or physiologically significant for a particular amphibian population depends on a variety of factors that will vary across regions and taxa. The seasonal timing and magnitude of the precipitation decrease will be important. Small precipitation decreases during the wet season, for example, in regions that currently experience large amounts of wet-season precipitation may not significantly affect amphibian populations, whereas decreases during the dry season could be much more significant. In our analysis, the precipitation decrease for a grid cell in one season was sometimes offset by increased precipitation in another season such that the overall annual precipitation for the grid cell increased. Depending on local conditions and taxa, precipitation increases in one season could ameliorate the effects of precipitation decreases in another season. The overall impact of precipitation decreases on amphibian populations will also depend on the timing and magnitude of accompanying temperature changes.

Precipitation is difficult for AOGCMs to accurately simulate, particularly for tropical regions (Dai 2006). Thus, our precipitation analysis identified western hemisphere ecoregions where multiple AOGCMs simulate decreased seasonal precipitation, but additional analyses are needed to determine the relevance of these changes to particular amphibian populations and to better assess the uncertainties in the AOGCM simulations.

Climate change is one of the largest challenges facing land managers and conservation planners. Addressing effects of climate change on amphibians, organisms that are tightly tied to specific microclimatic conditions and hydrological regimes and have limited dispersal abilities, will be particularly challenging. The challenge lies not only in the magnitude of change that is projected, but also in the uncertainty surrounding those projections. By combining assessments of vulnerability that take into account a wide range of climate-change projections with assessments that are independent of projected climate changes (e.g., the distribution of restricted-range species), we have provided an assessment of where, in the western hemisphere, amphibians are most likely to be vulnerable to climate change. Such assessments are a necessary first step for allocating scarce conservation resources at broad spatial scales.

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Supporting Information

A table of AOGCMs from which climate projections were derived (Appendix S1) and a list of amphibian species for which bioclimatic models were built (Appendix S2) are available as part of the on-line article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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