

Climate Change, Elevational Range Shifts, and Bird Extinctions

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Abstract: Limitations imposed on species ranges by the climatic, ecological, and physiological effects of elevation are important determinants of extinction risk. We modeled the effects of elevational limits on the extinction risk of landbirds, 87% of all bird species. Elevational limitation of range size explained 97% of the variation in the probability of being in a World Conservation Union category of extinction risk. Our model that combined elevational ranges, four Millennium Assessment habitat-loss scenarios, and an intermediate estimate of surface warming of 2.8° C, projected a best guess of 400–550 landbird extinctions, and that approximately 2150 additional species would be at risk of extinction by 2100. For Western Hemisphere landbirds, intermediate extinction estimates based on climate-induced changes in actual distributions ranged from 1.3% (1.1° C warming) to 30.0% (6.4° C warming) of these species. Worldwide, every degree of warming projected a nonlinear increase in bird extinctions of about 100–500 species. Only 21% of the species predicted to become extinct in our scenarios are currently considered threatened with extinction. Different habitat-loss and surface-warming scenarios predicted substantially different futures for landbird species. To improve the precision of climate-induced extinction estimates, there is an urgent need for high-resolution measurements of shifts in the elevational ranges of species. Given the accelerating influence of climate change on species distributions and conservation, using elevational limits in a tested, standardized, and robust manner can improve conservation assessments of terrestrial species and will help identify species that are most vulnerable to global climate change. Our climate-induced extinction estimates are broadly similar to those of bird species at risk from other factors, but these estimates largely involve different sets of species.

Keywords: biodiversity, avian biogeography, extinction likelihood, GIS, global warming, lapse rates, macroecology, mountain endemics, ornithology, tropical forests

Cambio Climático, Desplazamiento de Rangos Altitudinales y Extinciones de Aves

Resumen: Las limitaciones en la distribución de especies impuestas por los efectos climáticos, ecológicos y fisiológicos de la altitud son determinantes importantes del riesgo de extinción. Modelamos los efectos de los límites altitudinales sobre el riesgo de extinción de aves terrestres, 87% del total de especies de aves. La limitación altitudinal del rango de distribución explicó 97% de la variación en la probabilidad de estar en una categoría de riesgo de extinción de la Unión Mundial para la Conservación (IUCN). Mediante un modelo que combinó limitaciones altitudinales, escenarios de pérdida de hábitat de la Evaluación 4 Milenio y una estimación intermedia de calentamiento superficial de 2.8° C, se estimaron entre 400 y 550 extinciones de aves terrestres y que aproximadamente 2500 especies adicionales estarían en riesgo de extinción en 2100. Para aves terrestres del Hemisferio Occidental, las estimaciones de extinciones intermedias basadas en cambios inducidos por el clima en las distribuciones actuales variaron entre 1.3% (calentamiento: 1.1° C) y 30.0% (calentamiento: 6.4° C) de estas especies. A nivel mundial, cada grado de calentamiento proyectó un incremento no lineal en las extinciones de 100 a 500 especies. Solo 21% de las especies cuya extinción se pronosticó en nuestros escenarios están consideradas como amenazadas de extinción actualmente. Escenarios diferentes de pérdida de hábitat y de calentamiento superficial pronosticaron futuros sustancialmente diferentes para las

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especies de aves terrestres. Para mejorar la precisión de las estimaciones de extinciones inducidas por el clima, hay una urgente necesidad de medidas de alta resolución de los desplazamientos de los rangos altitudinales de las especies. Dada la acelerada influencia del cambio climático sobre la distribución y conservación de especies, el uso de límites altitudinales en una forma probada, estandarizada y robusta puede mejorar las evaluaciones de conservación de especies terrestres y ayudará a identificar especies que son más vulnerables al cambio climático global. Nuestras estimaciones de extinciones inducidas por el clima son similares a las de especies en riesgo por otros factores, y principalmente involucran diferentes conjuntos de especies.

Palabras Clave: biogeografía, bosques tropicales, calentamiento global, endémicos de montaña, SIG, tasas de abatimiento

Introduction

Habitat loss and global climate change threaten the survival of large fractions of species. The key questions are how many species do these factors threaten and to what extent do they involve the same or different species? Geographical range size is a fundamental criterion for determining when a species faces a heightened risk of extinction (i.e., a species is globally “threatened” or “near threatened” [BirdLife International 2000; IUCN 2001]). Small range size is the single best predictor of extinction risk for terrestrial species (Manne et al. 1999; Harris & Pimm 2007). Simply, with large-scale changes in land use (e.g., deforestation), it is easier to entirely eliminate a species with a small range than a large one. Estimates of changes in range size are used regularly to predict extinctions due to habitat loss or climate change (e.g., Thomas et al. 2004; Pimm et al. 2006).

Nevertheless, hardly any species is found throughout its mapped geographical range (Jetz et al. 2007), and habitat and elevational limitations can substantially restrict a species range size (Harris & Pimm 2007). Most organisms are confined to specific elevational bands as a result of microclimatic constraints imposed by ambient temperature and humidity on species metabolisms (Weathers 1997; McNab 2003) and on their preferred vegetation types (Martin 2001). These elevational limits have important ecological (Patterson et al. 1998; Martin 2001; Gage et al. 2004), evolutionary (Jetz et al. 2004), physiological (McNab 2003), and conservation (Gage et al. 2004; Pounds et al. 2006; Harris & Pimm 2007) implications. This is especially the case for highland species that are sensitive to climate change (Pounds et al. 1999; Williams et al. 2003; Pounds et al. 2006) and more likely to be at risk of extinction because of it (Gage et al. 2004; Pimm et al. 2006). Warming temperatures force many montane species uphill and reduce their ranges, sometimes entirely (Shoo et al. 2005b). Consequently, although habitat loss has primarily threatened lowland species, highland species in intact habitats are now facing the additional threat of warming temperatures that increasingly push

these species toward mountain tops (Williams et al. 2003; Pimm et al. 2006).

Despite the conservation significance of range size, however, considerable uncertainty accompanies many species actual distributions (Jetz et al. 2007). Often, the only information available is the extent of occurrence (EOO), “the minimum convex polygon drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy” (IUCN 2001). A more accurate estimate of global range size is the area of occupancy (AOO), the occupied area within a species EOO (IUCN 2001). A species AOO is often much smaller than its EOO and is critical for estimating extinction likelihood. Nevertheless, because of the lack of high-resolution data, the AOOs of most species are unknown, including 98% of bird species (BirdLife International 2006), the best-known order.

The resolution of range maps is critical because the AOO of one species can be orders of magnitude smaller than that of another species with the same EOO but a wider elevational range. It is difficult to have a grid resolution fine enough to be sensitive to elevational variation and yet coarse enough to be practical in avoiding excessive range underestimation (IUCN 2001). Coarse resolutions, often unavoidable due to the lack of data, can overestimate distributions (Jetz et al., in press), mask changes in elevational ranges and underestimate declines caused by climate change (Thomas et al. 2006). Furthermore, for about 1800 bird species, best EOO estimates vary by an order of magnitude, and for another 900 species, by twofold or more. The EOOs of about 1500 additional species, mostly near threatened, have not been estimated (BirdLife International 2007).

An overestimate of a species EOO leads to an underestimate of its extinction likelihood (Fig. 1a). Narrower elevational range often means a smaller EOO, which means higher extinction risk (Manne & Pimm 2001; Harris & Pimm 2007). Furthermore, because mountains narrow with increasing elevation, EOOs of highland species are often substantially smaller than those of lowland species with equally wide elevational ranges. Because a smaller

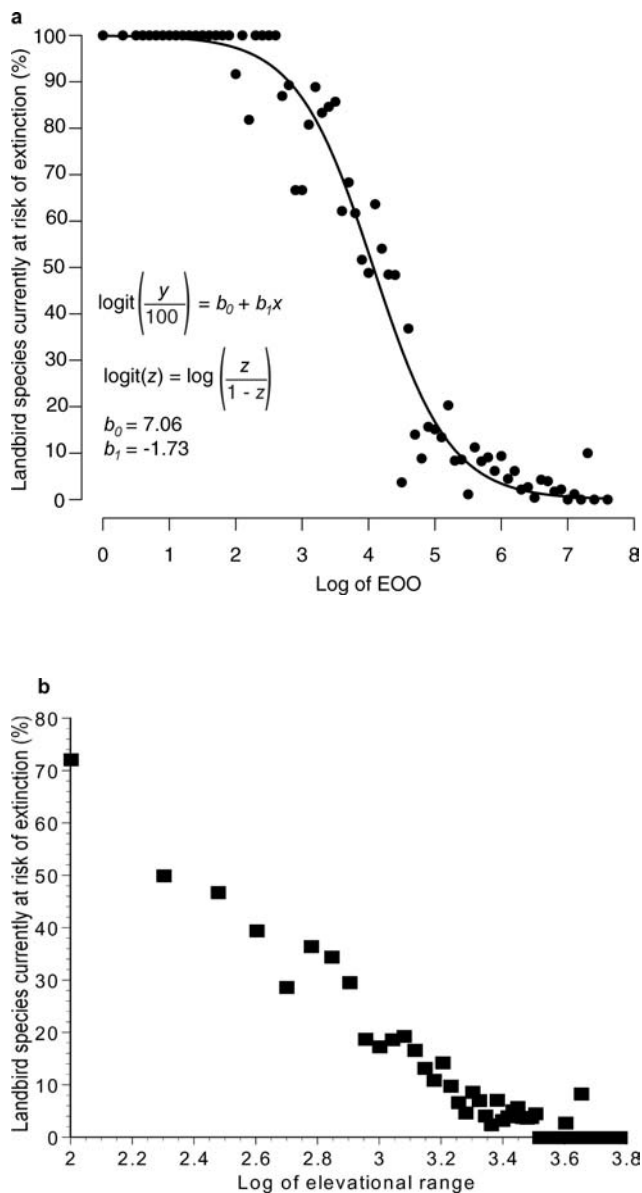


Figure 1. The relationship between bird extinction risk and (a) extent of occurrence ($r^2=0.88$, $p < 0.0001$) and (b) elevational range ($r^2 = 0.97$, $p < 0.0001$). In (a), the x-axis is the \log_{10} of each species extent of occurrence (BirdLife International 2007) rounded up to the nearest tenth, and the y-axis is the percentage of species in each extent-of-occurrence (EOO) category that faces a risk of extinction (threatened or near threatened). In (b), the x-axis is the \log_{10} of each species elevational range rounded up to the nearest hundred meters (upper elevational limit - lower elevational limit). For example, the point corresponding to 2 (= log of 100 m) on the x-axis means that of the 79 bird species that have elevational ranges that are ≤ 100 m, 72% are threatened or near threatened with extinction. (Also see Supplementary Material.)

EOO is highly correlated with increased extinction risk (BirdLife International 2000; IUCN 2001) (Fig. 1a), elevational ranges have high conservation significance (Fig. 1b) and acquire further importance under the prospect of climate change (Root et al. 2003; Williams et al. 2003; Thomas et al. 2004; Thomas et al. 2006). Thus, obtaining better knowledge of actual ranges and of species capacities to find suitable habitats as climate changes is a major conservation challenge. Better incorporation of elevational limits into assessments of extinction risk will increase the accuracy of range estimates, and, can bring to light potentially threatened species whose range or population sizes are unknown.

We calculated the relationship between conservation status (threatened or near threatened species, which we collectively define as "at risk of extinction") and the elevational limits of 8459 species of landbirds. Because birds are better known than any comparable group, our analysis is also a test of the potential usefulness of elevational limits for estimating extinction likelihoods of other terrestrial taxa, for which there is much less information.

We then estimated the effects of elevational limit shifts induced by climate change on the future conservation status of landbirds. Global increases in temperature (IPCC 2007) and consequent changes in water availability (Pounds et al. 1999; Still et al. 1999), in combination with ecological (Pounds et al. 1999; Martin 2001), physiological (Weathers 1997; Root 1988; Martin 2001; McNab 2003), and epidemiological (Benning et al. 2002; Pounds et al. 2006) limitations, are leading to upward shifts in many habitats and their associated species (Pounds et al. 1999; Parmesan & Yohe 2003; Williams et al. 2003; Bohning-Gaese & Lemoine 2004; Wilson et al. 2005; Franco et al. 2006; Thomas et al. 2006; Peh 2007). Populations of many highland taxa will likely decrease as global warming forces them to move to higher elevations (Pounds et al. 1999; Shoo et al. 2005a), resulting in reductions in range size and leading to greater extinction risk (Thomas et al. 2004, 2006), particularly where there is no land or habitat available at higher elevations (Benning et al. 2002; Williams et al. 2003; Pimm et al. 2006).

To project the impacts of climate-induced range changes on the EOOs of birds by 2100 and to estimate the number of bird species that would be extinct or would be at risk of extinction (threatened or near threatened) as a result, we modeled each species elevational limits for 60 scenarios consisting of unique combinations of five estimates of surface warming (IPCC 2007), four estimates of habitat loss on the basis of four Millennium Assessment scenarios (MA 2005), and three estimates of shifts in elevational limits. We also modeled the effects of these scenarios on the actual distributions (EOOs) of 3349 species of landbirds of the Western Hemisphere and then used these extinction estimates to calibrate our global estimates on the basis of elevational limits only.

Methods

Data

The data we used (see Supplementary Material for additional information) came from Ridgely et al. (2005), BirdLife International (2007), and a global bird-ecology database created for a previous study (Sekercioglu et al. 2004). A sample data set is available from www.pnas.org/content/vol0/issue2004/images/data/0408049101/DC1/08049DataSet1.xls.

Elevational versus Other Variables

We used multiple regression with model selection (Burnham & Anderson 2002) to examine the influence of key variables on a species probability of being threatened, being at risk, or going extinct (Supplementary Material). We used all combinations of possible explanatory variables, and, where appropriate, three interaction terms with both Akaike (AIC) and Bayesian information criteria (BIC) to compare models. To model threat and risk we used a generalized linear model with a binomial sampling distribution and a logistic link. To model the future extinction likelihood we used a generalized linear model with a Poisson sampling distribution and a log link. All analyses were performed in R 2.1.0 (R Development Core Team 2007) with scripts written by the authors.

To find the best-fitting equations linking elevational range to the percentage of species threatened and the percentage of species at risk, we fitted five linear models with normally distributed error terms. Because the BIC penalizes more harshly for model complexity and is a better evaluator for large sample sizes (Link & Barker 2006), we used BIC to compare the models. Minimum BIC was obtained with the second-order model (see later; Fig. 1b).

Climate-Change Scenarios

We based surface-warming estimates on the projected (between 2090–2100) “likely” range of working group 1 of the Fourth Intergovernmental Panel on Climate Change (IPCC) Assessment Report (IPCC 2007) for six emissions scenarios. The IPCC defines *likely* as 66% probability, so there is a 17% chance in either direction that surface warming will be $<1.1^{\circ}\text{C}$ or $>6.4^{\circ}\text{C}$. We used the lowest (1.8°C) and highest (4.0°C) best guesses, the average of the best guesses from six scenarios (2.8°C), and the extreme values (1.1°C and 6.4°C). Although these values are global averages and warming is expected to be higher on land and at high latitudes, 6.4°C covers the range of highest expected warming on land everywhere outside the Arctic, where there are no endemic species of landbirds (i.e., found only north of the Arctic Circle).

The lapse rate of temperature is the rate of air temperature decrease with increasing elevation. Almost all bird species experience values below $7^{\circ}\text{C}/\text{km}$ and most land

bird species reside in humid tropical areas, land, where $4\text{--}5.5^{\circ}\text{C}/\text{km}$ is the norm (Gaffen et al. 2000; Stone & Carlson 1979). Therefore, we used $5^{\circ}\text{C}/\text{km}$ for tropical birds and $6.5^{\circ}\text{C}/\text{km}$ for species with temperate, boreal, or cosmopolitan distributions. These values are also consistent with field measures (Shoo et al. 2005b) and the expected upslope shift in tropical montane cloud forests (a shift of $155\text{--}223\text{ m}/1^{\circ}\text{C}$, corresponding to lapse rates of $6.45\text{--}4.48^{\circ}\text{C}/\text{km}$ (Still et al. 1999).

There are few data on the potential extent and magnitude of current and future shifts in the elevational limits of bird species in response to climate change (Bohning-Gaese & Lemoine 2004; Shoo et al. 2006). Nevertheless, a lapse rate of $5^{\circ}\text{C}/\text{km}$ and 2.8°C surface warming implies that a bird species has to move up 560 m ($2.8/5\text{ km}$) to maintain its original habitat temperature and associated vegetation, presuming there are still land and suitable habitat available higher up. Nevertheless, in many places the maximum elevation is lower than the elevation a bird species needs to colonize in response to climate change. Furthermore, natural habitats are experiencing yearly reductions of 1.1% on average (Jenkins et al. 2003) and most habitats are expected to keep declining (MA 2005). Consequently, even if there is land higher up, there may not be suitable habitat.

Therefore, we used four habitat-change scenarios (MA 2005) to calculate the likelihood, for each habitat type, that a bird species would not be able to move up in response to climate change due to the lack of that habitat. We assumed that habitats would continue to decline or increase between 2050 and 2100 at the 2000–2050 rates of change. We calculated the habitat-loss percentages for all habitat types. For each habitat we randomly selected an equivalent percentage of bird species found in that habitat. The upper limits of these bird species remained fixed, to simulate the lack of habitat higher up, but lower limits could move up in response to climate change.

For example, based on the global-orchestration scenario, tropical forests are expected to decline 15% between 2000 and 2050 (MA 2005). Extrapolated to 2100, this means a reduction of 27.75% between 2000 and 2100. Thus, in our model, a bird species whose primary habitat is tropical forest has a 27.75% chance of not being able to go any higher in response to climate change. Therefore, in each simulation, the upper limits of 27.75% of randomly selected species of tropical forest birds were not permitted to go any higher. This percentage varied for each combination of habitat type, habitat loss scenario, and climate-change estimate. For example, corresponding loss of tropical forest estimates were 22.4% in “order from strength,” 10.9% in “adaptive mosaic,” and 11.3% in “technogarden” scenarios.

For a species whose upper limit was assumed to remain fixed because of the lack of habitat, if predicted surface warming forced the lower limit of the species to equal or exceed its upper limit, this was recorded as an

“extinction.” Species that kept to their lower elevational limits retained or expanded their ranges and therefore suffered no “extinctions.” Those that were unable to expand their upper limits due to the lack of terrain or habitat could “go extinct” because of the probability of their lower limits exceeding their upper limits.

Birds living in hotter and drier habitats often show physiological adaptations, such as reduced thermal conductance (Weathers 1997; Seavy 2006), lower evaporative water loss (Weathers & Green 1998), and higher heat tolerance (Weathers 1997; Weathers et al. 2001). Therefore, lowland bird species, adapted to higher temperatures, are likely to tolerate temperature increases better than highland species (Weathers 1997). Furthermore, lower elevational-range boundaries in humid regions are probably shaped more by complex biotic interactions and may be less likely to shift under changing climate than upper limits (Bohning-Gaese & Lemoine 2004). Because the cutoff point between lowland and highland avifauna is approximately 500 m (Patterson et al. 1998) and because highland species are more sensitive to climate-change-induced weather patterns (Pounds et al. 1999) and emerging diseases (Benning et al. 2002; Pounds et al. 2006), species living above 500 m are more sensitive to climate change. Thus, we assumed that all of these species lower elevational limits would go up in response to surface warming. Some climatically tolerant species will remain in the lowlands despite increasing temperatures, although the proportion is hard to predict. Therefore, for best-case scenarios we assumed that none of the species living below 500 m would shift their lower limits upward. For intermediate scenarios we assumed half the species would shift their lower limits upward, and for worst-case scenarios we assumed all lowland species would shift their lower limits upward.

Because there were no data we were aware of to guide us in the selection of these values, we explored the entire response space (0%, 50%, and 100%) in order to bracket uncertainty and to understand how much our lack of knowledge of these characteristics matters. Because the sensitivity to this parameter is strictly linear (see later), the number of extinctions corresponding to other values can be calculated based on the three estimates we gave for each scenario. For each scenario we reported extinction estimates based on the average of 100 model runs because the running average of extinction estimates stabilized around 50 runs (Supplementary Material).

Elevational range is strongly correlated with the percentage of species at risk of extinction (Fig. 1b). Thus, after calculating each species new elevational limits based on different scenarios, we combined future elevational range estimates with the best-fit equation ($r^2 = 0.97$) that describes the elevational range-extinction risk function in Fig. 1b to calculate the resulting numbers of species that would be at risk of extinction in 2100 according to each scenario. The equation had the form

$$y \sim \text{binom}(n, p) \quad \text{invlogit}(x) = \frac{e^x}{1 + e^x}, \quad (1)$$

$$p = \text{invlogit}(f(E)) \quad f = b_0 + b_1E + b_2E^2$$

where y is the number of threatened or at-risk species; n is the number of species; E is the log elevational range; $b_0 = 0.694$, $b_1 = 0.6674$, and $b_2 = -0.142$ for at-risk species.

For example, a species whose current elevational range is 1000 m has an 18.6% probability of being at risk (threatened or near threatened). With a lapse rate of 5.0° C/km, if that species shifted its lower limit up by 560 m to compensate for an increase in surface temperature of 2.8° C (2.8/5.0 km shift) but was unable to go any higher because there was no habitat available, its elevational range would shrink. The consequent reduction in its elevational range to 440 m would mean that this species would have a 37.5% probability of being threatened or near threatened. Summing these probabilities across all species, we estimated the total number of bird species that would be at risk of extinction based on each scenario.

Western Hemisphere Birds

Because the global distribution maps of Western Hemisphere bird species are publicly available (Ridgely et al. 2005), we calculated future extinctions expected to result from the projected changes in the mapped EOOs (Ridgely & Tudor 1989, 1994; Ridgely et al. 2005) of Western Hemisphere birds. Birds do not nest above 6500 m. The Western Hemisphere, where the range in elevation is from -86 m to 6959 m and where over two-fifths of the world's bird species reside, is highly representative of the topographical and ornithological diversity of the planet. Western Hemisphere extinction estimates of 60 elevation-only scenarios correlated highly ($r^2 = 0.99$, $p < 0.0001$) with the same scenarios' extinction estimates of all species of landbirds.

We calibrated our elevation-based estimates of all extinct and at-risk species by (1) calculating the effects of projected elevational limit shifts by 2100 on the current estimated distributions (digitized EOOs) of 3349 species of Western Hemisphere landbirds, (2) estimating the numbers of Western Hemisphere species that would be extinct or at risk of extinction as a result of changes in their EOOs, and (3) comparing the results of steps 1 and 2 with Western Hemisphere estimates of at-risk and extinct species on the basis of only elevational limits in 2100. (Additional details are available in Supplementary Material.)

In step 2 we calculated the number of Western Hemisphere species facing a risk of extinction by feeding their estimated future EOOs into the following equation ($r^2 =$

0.88, $p < 0.0001$; Fig. 1a):

$$\begin{aligned} &\text{logit (proportion of species at risk of extinction)} \\ &= 7.06 - 1.73 * \log(\text{EOO}). \end{aligned} \quad (2)$$

In step 3 we calculated the ratio of the area-based estimate of at-risk species to the elevation-based estimate; the latter was calculated with the Eq. 1, which describes Fig. 1b. We used the resulting numbers to calibrate the estimates of at-risk species in the corresponding global scenarios that used elevational ranges only. We used multiple regression to calculate the contribution of elevational range, EOO, and other key variables (see Supplementary Material for additional information) to future extinction likelihood and compared models with both AIC and BIC as detailed earlier. To model the frequency of simulated future extinctions, we used a generalized linear model with a Poisson sampling distribution and a log link.

Results

Extinction risk increased rapidly at EOO values of 10,000 km² or lower (Fig. 1a), in close agreement with the recent findings of Harris and Pimm (2007). Species with wider elevational ranges were less likely to be threatened ($r^2 = 0.97$, $p < 0.0001$; Supplementary Material), near threatened ($r^2 = 0.88$, $p < 0.0001$), or either (at risk of extinction; $r^2 = 0.97$, $p < 0.0001$; Fig. 1b). When threat categories were analyzed separately, elevational range was also correlated negatively with the likelihood of being vulnerable ($r^2 = 0.88$, $p < 0.0001$), endangered ($r^2 = 0.88$, $p < 0.0001$), or critically endangered ($r^2 = 0.95$, $p < 0.0001$).

Sensitivity Analyses

When we recalculated the elevational range-conservation status relationship for all the bird species, including water birds, but excluding data-deficient species, r^2 was 0.95 ($p < 0.0001$), both with or without 38 extinct bird species with known elevational limits. Excluding only seabirds (but including coastal, wetland, and riparian species; $r^2 = 0.95$; $p < 0.0001$), sea and coastal birds ($r^2 = 0.96$; $p < 0.0001$), or sea, coastal, and wetland birds ($r^2 = 0.97$; $p < 0.0001$) made little difference. The r^2 was 0.92 ($p < 0.0001$) when we used extreme rather than the typical elevational limits. When we excluded species with elevational distributions estimated as 0–500 m (lowland) and 500–1000 m (foothill) because of the lack of detailed information, r^2 remained 0.97 ($p < 0.0001$). The relationship between elevational range and conservation status was not driven by a few threatened bird species with narrow elevational ranges. Even when we excluded more than a quarter of the land bird species with the narrowest elevational ranges, r^2 was 0.91 ($p < 0.0001$), and it was 0.88 ($p < 0.0001$) when we excluded more than half (Supplementary Materials). Therefore, the relation-

ship between elevational range and conservation status was a robust one that was not sensitive to our choices of certain criteria.

Extent of Occurrence versus Elevational Range

EOO (one of the main IUCN criteria for determining conservation status; BirdLife International 2000; IUCN 2001) was highly correlated with being at risk ($r^2 = 0.88$, Fig. 1a). If EOO is also highly correlated with elevational range, this may result in the strong relationship between elevational range and conservation status. Nevertheless, the correlation between the elevational ranges of 7762 land bird species and their EOOs was not high ($r^2 = 0.270$).

The performance of the models predicting the percentages of bird species threatened or at risk (near threatened or threatened) is summarized in Supplementary Material. The same models were selected for predicting both threat and risk. Under AIC the best model included all elevational variables and interactions with EOO. The BIC, which penalizes more heavily for model complexity, discarded the variables “midpoint” and “maximum of elevational range.” Although EOO was the variable that dominated these models that predicted extinction risk, elevational variables such as elevational range were also important. This was also the case for models that predicted future bird extinctions (Supplementary Material), which confirms the value of using elevational ranges to predict extinctions. Identical elevational-shift assumptions resulted in 1.3–5.3 times more extinctions among Western Hemisphere birds when EOOs were taken into consideration simply because actual topography may not allow an upper-limit shift even if an elevation-only scenario does.

Effects of Climate Change on Landbirds

Intermediate scenarios (surface warming 2.8° C by 2100 and 50% of lowland [≤ 500 m] species assumed to move up their lower limits in response to warming) projected approximately 400–550 bird extinctions by 2100, depending on the Millennium Assessment scenario (Fig. 2a). The worst-case, order-from-strength scenario (MA 2005) combined with 6.4° C warming and all species lower limits moving up, projected about 2498 extinctions or 30% of all landbirds. An additional 1770–2650 species were predicted to be threatened or near threatened (Fig. 2b, current baseline = 1651 species). For Western Hemisphere landbirds intermediate extinction estimates based on projected climate-induced changes in current distributions (Ridgely et al. 2005) ranged from 1.3% (1.1° C warming) to 30.0% (6.4° C warming) of these species (Fig. 3). Only 21% of the species predicted to become extinct in our scenarios are currently considered threatened with extinction.

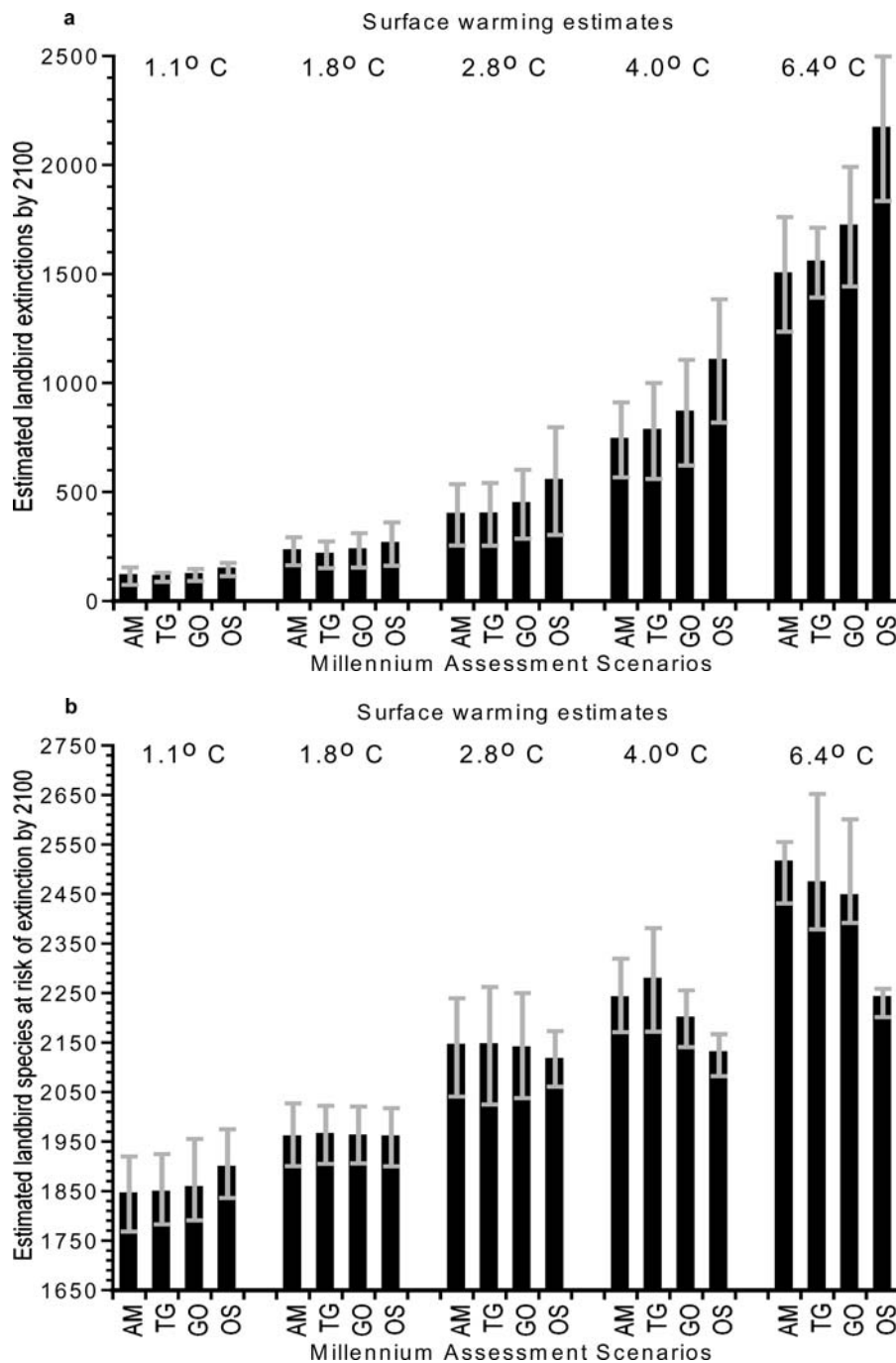


Figure 2. Number of world landbird species projected to be (a) extinct (current baseline = 0) or (b) at risk of extinction (near threatened or threatened; current baseline = 1651) by 2100 on the basis of estimates of various surface-warming estimates (IPCC 2007), three possible shifts in lower elevational limit, and Millennium Assessment habitat-change scenarios (MA 2005; AM, adaptive mosaic; GO, global orchestration; OS, order from strength; TG, technogarden). Bars show the results of an intermediate amount of elevational shift, where lower limits of 50% of lowland (≤ 500 m) bird species are assumed to move up in response to surface warming. "Error bars" indicate best-case (0% move up) or worst-case (100% move up) climate-warming scenarios (Methods).

For each of the four variables in the model we conducted a sensitivity analysis, changing one variable at a time while keeping others constant. We used AIC and BIC to evaluate the models with normally distributed error terms to find which order polynomial model fit the data best (all $r^2 > 0.99$, Supplementary Material). Number of bird extinctions was a quadratic function of surface-warming estimates (Fig. 2a; all $r^2 > 0.99$, $p < 0.0001$). A decrease in lapse rate resulted in a cubic increase in bird extinctions (Fig. 4). Percentage of species moving up their lower elevational limits had a positive, linear effect

on the number of bird extinctions, which was a negative fourth-degree function of the percentage of species shifting up their upper limits (Fig. 4).

Discussion

Elevational limits have substantial impacts on avian distributions and, consequently, on avian extinction risk. Results of previous studies show that elevational range

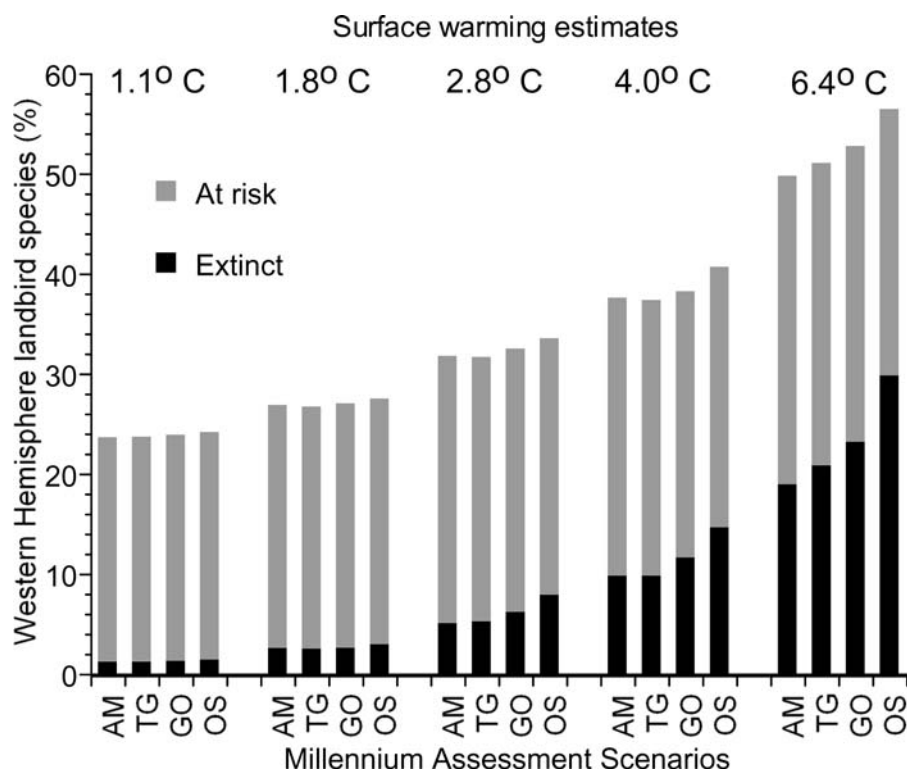


Figure 3. Number of Western Hemisphere bird species projected to be at risk of extinction or to be extinct by 2100. Estimates are based on the projected reductions in their current global ranges (EOOs) as a consequence of surface warming (IPCC 2007) and habitat change (MA 2005). In each scenario all lower limits >500 m shifted upward and 50% of lower limits ≤500 m shifted upward. Upper limits were allowed to shift or not depending on the combination of Millennium Assessment habitat change scenarios (see Fig. 2 legend for definitions of scenario abbreviations) and topography (see Methods).

affects conservation status (Manne & Pimm 2001; Gage et al. 2004). Thus, fuller consideration of elevational effects is essential for more-refined analyses of extinction risk, especially for disturbances such as climate change that can force substantial range shifts (Bohning-Gaese & Lemoine 2004; Thomas et al. 2006). The nonlinear relationship means that a few degrees of difference in surface warming could result in disproportionate increases in extinctions (Fig. 2a). Projected extinctions also increased rapidly (Fig. 4) at lower lapse rates (<6° C/km), typical of tropical areas where most of the landbirds, especially mountain endemics, are found. Furthermore, hundreds of predicted extinctions were of montane species that are currently not considered threatened or near threatened. Sedentary species living in lowlands with little vertical relief (e.g., Amazon and Congo basins, eastern Canada, western Australia) would also be affected because they would have nowhere to go. Migrating birds face lower risks of extinction than sedentary species (Sekercioglu 2007), and their mobility should make them less susceptible to climate-induced range limitations. As expected, in an intermediate scenario (technogarden, 2.8° C warming, 50% of lower limits shifting up), 5% of sedentary bird species were predicted to become extinct, whereas 1% of long-distance migrants were predicted to become extinct.

Caveats

There are many assumptions and simplifications implicit in our approach. Elevational limits vary regionally and

may even differ between the windward and leeward sides of the same mountain. Species do not respond uniformly in time or space to climate change (Bohning-Gaese & Lemoine 2004). Some species, especially migrating birds, will be able to adapt or shift their ranges horizontally. Lapse rates (Stone & Carlson 1979) and estimates of climate change (IPCC 2007) vary among the world's regions and even between different elevations in the same region (Schneider et al. 1978). Therefore, the numerical estimates from our broad-scale model are not intended to be taken literally to predict the bird extinctions or the future bird community of a specific location; such predictions should be based on local ecological and climate models (Peterson et al. 2001; Williams et al. 2003). Nevertheless, our global estimates demonstrate a framework that will generalize roughly to many local situations.

Implications of Elevational Limits

Despite our admonition not to take our model-dependent quantitative results literally at specific locations, the substantial correlation between elevational ranges and extinction likelihood and the robustness of this relationship to large changes in uncertain parameters (demonstrated by our sensitivity analyses) strongly suggest that climate-induced changes in elevational distributions will reduce the global ranges of many avian taxa (Bohning-Gaese & Lemoine 2004), frequently to the point of extinction. These results bolster our qualitative expectation that typically projected warming will lead to sizeable increases in the numbers of threatened and extinct bird

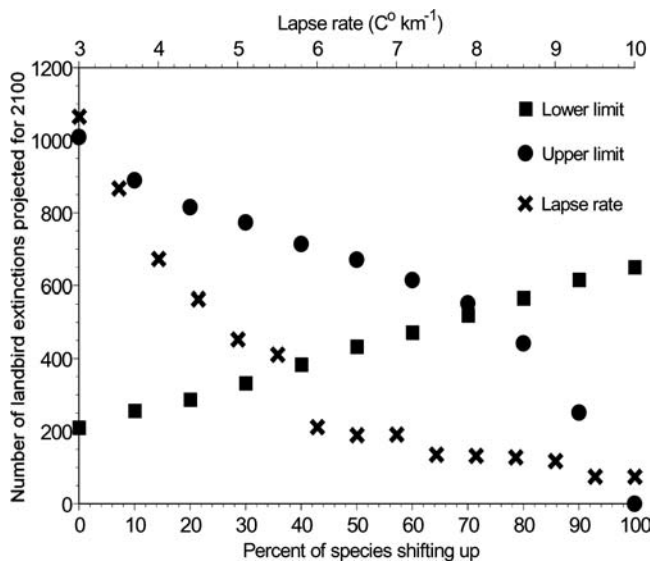


Figure 4. Sensitivity analyses of temperature lapse rates and lower- and upper-limit elevational range shifts on the numbers of projected bird extinctions for 2100. For each time step, 10% of lowland species are assumed to shift their lower elevational limits upward and be subject to a surface warming of 2.8°C and to restrictions on upper elevational-limit shifts based on the Millennium Assessment Technogarden scenario (MA 2005). For upper-limit sensitivity analysis we assumed a surface warming of 2.8°C and 50% of lowland species moving their lower limits upward. Lapse rate is the rate of air temperature decrease with increasing elevation. For lapse rate sensitivity analysis we assumed a surface warming of 2.8°C , 50% of lowland species moving up their lower limits, and restrictions on upper-limit shifts based on the technogarden scenario.

species. Climate change is increasingly causing upward shifts in the distributions of plant and animal species, but coarse-resolution distribution data can mask these shifts (Thomas et al. 2006). To obtain more realistic estimates of climate-change influence on extinction risk, such elevational effects must be accounted for more explicitly and at finer resolutions than is typical of most current analyses of conservation status.

Particularly urgent is the need for high-resolution (≤ 1 km) data on elevational limit shifts induced by climate change because these shifts can have substantial effects on future extinctions (Figs. 2a & 4). Better distribution data will also improve the knowledge of species ranges. The mapped ranges of many range-restricted, threatened, and specialized bird species are overestimates of their actual distributions (Harris & Pimm 2007; Jetz et al. 2008), which can lead to underestimates of these birds' extinction likelihoods. More funding needs to be allocated, especially in the tropics, to conduct comprehensive and

detailed surveys of bird species with narrow elevational ranges. We also need to make better use of the millions of observations being collected by rapidly increasing numbers of competent birdwatchers (Sekercioglu 2002). The same needs apply to other orders on which we have even fewer data.

The values we used to bracket global climatic variation were, if anything, conservative, particularly with respect to humid tropics and highlands. That is, lapse rate is lower than $5^{\circ}\text{C}/\text{km}$ in most of the former (Stone & Carlson 1979), and expected warming is higher in the latter (Schneider et al. 1978). Correspondingly, larger elevational shifts in these speciose areas with high endemism (BirdLife International 2007) will likely result in higher numbers of extinctions, a contention that is also supported by the nonlinear nature of surface warming and lapse-rate sensitivity analyses (Figs. 2a & 4). Although we used elevational distribution as a proxy for population size, in response to increasing temperatures highland bird populations can decline even faster than the areas they occupy (Shoo et al. 2005a). Many endemic bird species are confined to mountains (BirdLife International 2007), especially in the species-rich tropics, where pronounced climatic and ecological isolation between lowland and montane habitats (Janzen 1967) is likely to prevent the dispersal of numerous montane species to other areas. Tropical montane birds have higher metabolisms than their lowland counterparts (Weathers 1997; McNab 2003), and like other tropical montane vertebrates (Williams et al. 2003), might experience increased mortality from expected rises in surface temperatures.

The IPCC (2007) estimates are aggregates of land and sea-surface estimates and warming on land is expected to be higher. Some vegetation communities will be unable to keep up with rapid surface warming, particularly if suitable soils are absent from climatically suitable areas. Temperature increases are enabling the invasions of higher elevations by disease vectors that are expected to trigger bird extinctions (Benning et al. 2002). It is also disconcerting that 67% of the species predicted to become extinct in our models are not currently considered threatened or near threatened with extinction. Finally, climate change will affect some species more than others, leading to changes in species interactions (Martin 2001), decoupling of symbioses, and the destabilization and disassembly of communities (Root et al. 2003), all of which can result in cascading effects and further extinctions (Bohning-Gaese & Lemoine 2004; Sekercioglu et al. 2004).

Various factors affect avian extinction risk (BirdLife International 2000). Nevertheless, elevational range accounted for 97% of variation in the proportions of landbird species that face a risk of extinction (Fig. 1b). By adding a more-detailed and explicit treatment of elevational processes, calculating elevational range shifts also makes it possible to extend previous analyses and to

estimate the effects of climate change on the extinction risk of all landbirds. Given the uncertainties inherent in the factors involved, no one model can successfully predict climate-based extinctions in diverse parts of the planet. Only highly detailed regional models based on extensive data sets can provide more disaggregated estimates of the effects of climate change on individual species (Peterson et al. 2001; Shoo et al. 2005b). Nevertheless, these models require large quantities of standardized long-term data, which, for most species, are not available. Furthermore, although climate modelers note that three-dimensional climate models do exhibit some accuracy at individual grid points (Root et al. 2005), a broad consensus of climate scientists readily acknowledges that detailed local projections from climate models are less reliable than hemispherical or global aggregations (IPCC 2007). This is an equally strong caveat for climate-model projections of vertical temperature changes. Given the accelerating influence of climate change on species distributions and conservation (Parmesan & Yohe 2003; Root et al. 2003; Malcolm et al. 2006; Pounds et al. 2006), the more explicit inclusion of elevational processes is a vital component of conservation activities, at least for birds (Shoo et al. 2006).

Nevertheless, we suspect that similar approaches can also improve estimates of the effects of climate change on the extinction risk of other organisms. Although most species populations are not distributed uniformly across different elevations and climate-induced changes in abundance patterns have important conservation implications, these changes have not been well studied (Shoo et al. 2005a). Because our knowledge of the global distributions of nonavian taxa is typically more limited and most of these groups are more threatened than birds (Pimm et al. 2006; IUCN 2007), incorporating elevational distributions and related processes in a standardized manner could significantly improve conservation assessments of other terrestrial species and our ability to identify those that will be most vulnerable to climate change.

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Supplementary Material

Additional methods; influence of key variables on threat probability, risk probability, and frequency of simulated

future extinctions; AIC, BIC, and likelihood values; coefficients of the models in which being threatened or at risk is a function of log elevation range; coefficients for orders of the model that describe the sensitivity of future extinctions to model parameters; effects of reduced range size on likelihood of being threatened with extinction and sensitivity of this relationship to the accumulating exclusion of bird species with narrow elevational ranges; effect of the number of simulations conducted on the predicted number of extinctions for an intermediate scenario; fitted curves for the polynomials that predict the likelihood of being threatened or at risk as a function of elevational range and for the functions that describe the sensitivity analyses of model parameters are available as part of the on-line article from <http://www.blackwell-synergy.com/>. The author is responsible for the content and functionality of these materials.

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