



CLIMATE CHANGE

Climate change extinctions

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Climate change is expected to cause irreversible changes to biodiversity, but predicting those risks remains uncertain. I synthesized 485 studies and more than 5 million projections to produce a quantitative global assessment of climate change extinctions. With increased certainty, this meta-analysis suggests that extinctions will accelerate rapidly if global temperatures exceed 1.5°C. The highest-emission scenario would threaten approximately one-third of species, globally. Amphibians; species from mountain, island, and freshwater ecosystems; and species inhabiting South America, Australia, and New Zealand face the greatest threats. In line with predictions, climate change has contributed to an increasing proportion of observed global extinctions since 1970. Besides limiting greenhouse gases, pinpointing which species to protect first will be critical for preserving biodiversity until anthropogenic climate change is halted and reversed.

Climate change is altering species abundances, ranges, and interactions as well as ecosystems worldwide (1–3). Although evidence suggests that some species are tracking changing climates through dispersal (4, 5) or persisting through plasticity or adaptation (6, 7), other species face declining populations, range retractions, and possible extinctions (8, 9). This loss and rearrangement of biodiversity threatens not only ecosystems but biodiversity's many contributions to people (10). Enabling effective and efficient conservation efforts to protect biodiversity requires accurate projections under divergent emissions scenarios. Such predictions also can identify the species, ecosystems, and regions that face the greatest risks (11).

Recent global biodiversity assessments predict extinction risks for a million or more species, but the specific contribution from climate change remains uncertain (2). Prior studies that focused on climate change suggest a wide range of extinction risks contingent on different approaches, regions, taxa, and assumptions (8, 9, 12, 13). Global assessments report an increasing, but uncertain, extinction rate from climate change but omit recent, more sophisticated modeling efforts that better represent taxonomic and geographic diversity (3, 12).

I conducted a comprehensive assessment of predicted global extinction risks from climate change. Extinction risk is defined as a probabilistic estimate that a species will become extinct in the future without mitigation. I adopted climate science terminology and used “projections” to refer to predictions generated for specific emissions scenarios. This new analysis incorporates more than 5.5 million individual projections from 485 peer-reviewed multispecies studies, covers most known spe-

cies, and encompasses the work of 1425 scientists over three decades (supplementary text and tables S1 to S3). Current estimates not only triple the number of studies from past assessments but also rely on newer, more sophisticated modeling approaches that incorporate species' sensitivity and adaptability to climate change (11). New studies also better represent underanalyzed geographic regions, including Asia and Africa (8). This formal meta-analysis weights studies by inverse variance (number of species predicted); addresses taxonomic

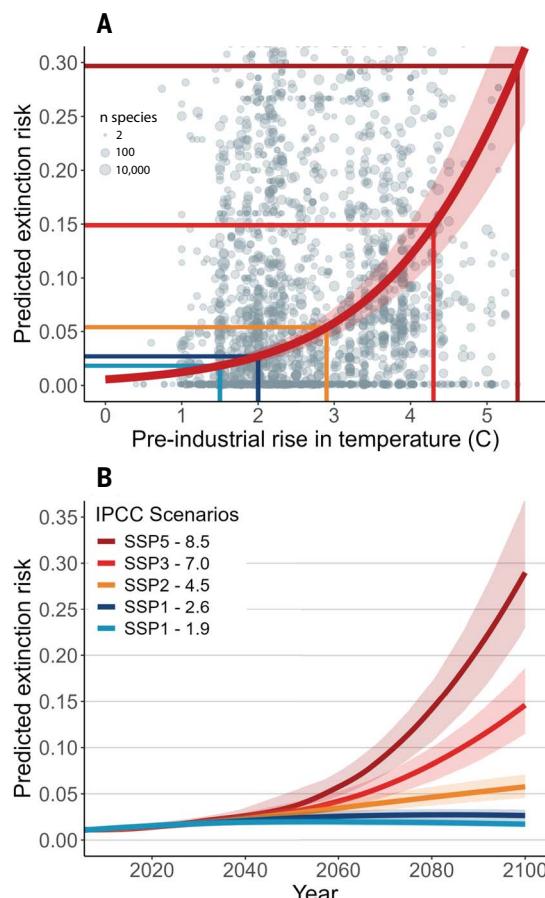
and geographic biases; integrates the relationship between extinction risk and habitat loss; develops predictions from the latest emissions scenarios; assesses relative contributions to elevated risks from geography, ecosystem, taxonomy, species traits, and modeling approaches and assumptions; and synthesizes observed extinctions attributed to climate change.

Global climate change extinctions

Global climate change is projected to threaten 7.6% of species with extinction [95% credible interval (CI₉₅): 6.6, 8.7%], averaged across all emissions scenarios and modeling assumptions. This CI encompasses the median from a 2015 global assessment, 7.9% (8). The sensitivity of extinction risk to temperature change did not vary substantially over time (fig. S13). What has changed is that uncertainty has decreased by up to 50%, especially for projections at higher temperatures (Fig. 1A and fig. S14).

Global extinction outcomes strongly depended on global emissions scenarios (Fig. 1, A and B). At current global temperatures ~1.3°C above the preindustrial average, 1.6% (CI₉₅: 1.2, 1.9%) of species are projected to become extinct (Fig. 1A). Extinction risks are projected to increase to 1.8% (CI₉₅: 1.5, 2.3%) at the 1.5°C

Fig. 1. Predicted proportional extinction risk from climate change relative to projected global temperature rise (°C). (A and B) The median predicted extinction risk trend with 95% CI (shaded region) is depicted relative to preindustrial (1850 to 1900) temperatures (A) in 2100 and (B) through time under different emissions and SSPs. The size of individual data points is proportional to the log number of predicted species. An extended version can be viewed in fig. S12.



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threshold advocated by the 2015 Paris Agreement and embodied by Shared Socioeconomic Pathway (SSP) 1-1.9. Beyond this threshold, extinction risks increase to 2.7% (CI_{95} : 2.2, 3.3%) at 2.0°C (SSP 1-2.6). Current international emission abatement commitments (14) would elevate global temperatures to 2.7°C, threatening 1 in 20 species. Beyond this temperature, extinction risks quickly accelerate to 14.9% (CI_{95} : 11.6, 18.8%) at 4.3°C (SSP 3-7.0) and 29.7% (CI_{95} : 23.0, 37.1%) at 5.4°C (SSP 5-8.5).

Regional and taxonomic diversity-corrected estimates did not differ substantially from uncorrected estimates because the projections for the most diverse regions and taxonomic groups were similar to global averages (figs. S9 to S11). Results were robust to publication biases; time periods; and alternative statistical models, transformations, priors, and distributions (supplementary text).

Explaining extinction risks

I separately evaluated six sets of factors expected to affect extinction risk estimates. The factors that explained the most variance in extinction risk predictions were geography (14.5%), ecosystem type (12.9%), modeling approach (11.6%), and threat level (11.2%) (Figs. 2 and 3 and table S7). Models accounting for these factors and the variance among studies explained more than 78% of the total variation.

Geography

Extinction risks varied across continents and major latitudinal zones. Australia/New Zealand

and South America were characterized by the highest risks at 15.7 and 12.8%, respectively, whereas Asia had lower risks (5.5%) (fig. S15). Across latitudinal zones, lower extinction risks were projected for the north temperate and Arctic latitudes (6.4 and 3.8%, respectively) (fig. S16). A finer-scaled regional analysis that combined continents and latitudinal zones produced the best-supported geographic model (Fig. 2 and fig. S17). This regional model reinforced the higher threats to South America, Australia, and New Zealand and lower threats to Arctic Europe and also indicated higher extinction risks for northern Africa (17.4%; CI_{95} : 9.0, 31.1%). A moderate extinction risk of 6.1% (CI_{95} : 3.4, 10.7%) was predicted for the oceans.

The results emphasize extinction risks in Australia and New Zealand, where many terrestrial species can only track climate change so far before encountering the sea (15, 16). The high extinction risks in South America likely reflect projected losses from hyperdiverse biodiversity hotspots inhabited by species with small ranges and specialized niches, facing no analog climates, and which are already declining from habitat loss (17, 18). Few studies previously characterized risks in Africa and Asia, but new studies indicate moderate risks for these continents, except for northern Africa, where risks were higher. Of the studies, 44% were conducted in North America and Europe, which were characterized by moderate risks overall and lower Arctic risks (3 to 5%). High-latitude species from the Arctic are generally characterized by larger range sizes [Rapoport's rule

(19)], and species with larger ranges are often more resilient to disturbance (20). Also, northern species can colonize and track climate change into the expansive northern lands that are steadily becoming suitable for warmer-adapted species, although this does not protect the northernmost species or species that depend on declining Arctic Sea ice. By contrast, in the Southern Hemisphere, most land masses narrow at higher latitudes, suggesting how an artifact of terrestrial geometry might generate divergent extinction rates between hemispheres. Many species are still highly threatened in regions with lower overall mean risks, and thus, regional averages should not preclude attention to these regions and species.

Taxonomy

Extinction risks did not differ among taxonomic groups in a previous assessment likely because most models ignored the taxon-specific traits that would differentiate taxonomic responses (8, 11). More mechanistic studies can now distinguish risks across taxonomic groups (Fig. 3). Amphibians were projected to face higher-than-average risks (10.0%; CI_{95} : 7.6, 13.2%). Amphibians might be vulnerable to climate change given their biphasic life histories, low dispersal abilities, endangerment from other threats, sensitivity to weather, and association with freshwater ecosystems characterized by high climate risks (21, 22). Birds, meanwhile, were predicted to face lower risks (5.5%; CI_{95} : 4.5, 6.7%). Many birds disperse well, which can facilitate range expansion during climate change (5), and

Fig. 2. Predicted extinction risks by region.

Colors are proportional to the median extinction risks in the legend, and 95% CIs are displayed in their respective colors. The median is displayed in white or blue along with an upward- or downward-facing triangle when its 95% CIs occur above or below the global median of 7.6%, respectively. The number of studies (N) and model variations (n = iterations within studies based on varying assumptions) are included under each estimate. Data-deficient regions are displayed in gray.

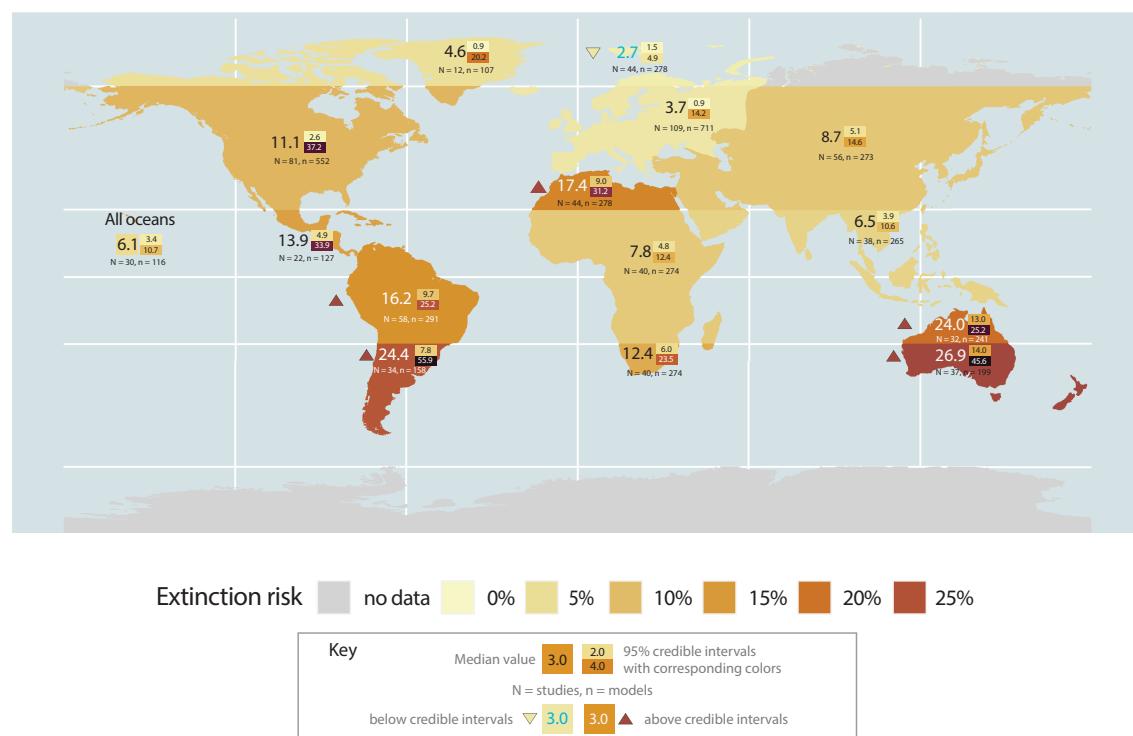
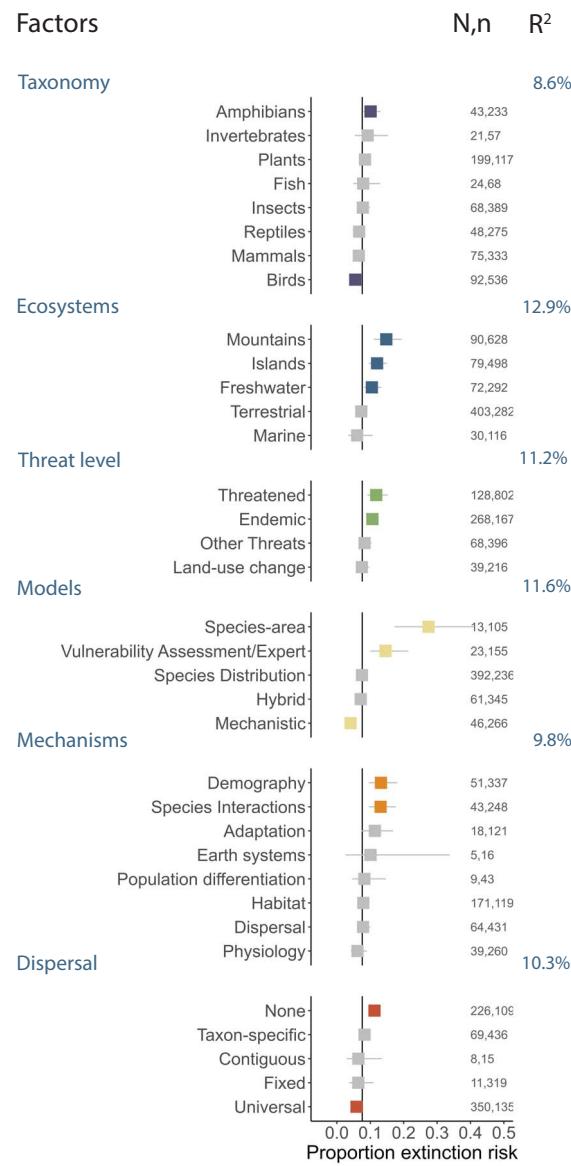


Fig. 3. Factors contributing to extinction risk variation. Each symbol indicates the median estimate, and error bars indicate 95% CIs. Colored symbols indicate factors with CIs that do not overlap the median extinction risk (7.6%), which is displayed as a vertical line. The number of studies (N), model variations (n), and variance explained by each set of factors [Bayesian coefficient of determination (R^2)] are displayed to the right of each estimate.



some species have adapted to climatic changes (23). However, care should be taken not to generalize too much; species within each taxonomic group can still be highly threatened, and therefore, taxonomic generalities should not supersede species-specific predictions.

Ecosystems

Threats to specific ecosystems explained the second most variance in extinction risks (12.9%). Species from mountain, island, and freshwater ecosystems were characterized by high extinction risks (Fig. 3). Threats to mountain species were especially elevated at 14.8% (CI_{95} : 11.0, 19.3%), reflecting the concern that climate change can put mountain species onto “an escalator to extinction,” in which species track climate change up to the mountain peak until they have nowhere else to go (24, 25). Island species also faced higher risks of 12.0% (CI_{95} : 9.6, 15.0%), likely because of smaller population

sizes, preexisting threats such as from invasive species, and a limited geographic area to track climate change relative to continental species (15). Freshwater species also were characterized by higher risks (10.5%; CI_{95} : 8.1, 13.3%). Freshwater species are often dispersal-limited and already declining from pollution, invasive species, and water extraction (26, 27). Terrestrial and marine species were threatened at median levels.

Threat level

Some studies focused on species expected to face higher threats from climate change *a priori* because of specific traits (for example, poor dispersers), risky habitats (such as mountains), or exposure to additional threats such as habitat loss. These studies indeed estimated risks ~4% higher than the median (11.8%; CI_{95} : 9.1, 15.2%) (Fig. 3). Studies on endemic species, which are defined as species with ranges contained within the study area, estimated higher

risks of 10.6% (CI_{95} : 8.8, 12.5%). Endemic species generally have smaller ranges, which consistently are predicted to suffer higher climate change extinction risks (20, 28). Contrary to predictions, models that included other threats such as current and future land use did not produce higher-than-normal risks. Although surprising, this result depends on model assumptions about future land-use policies that might both increase and diminish future risks. More research is needed to understand when land-use change acts synergistically with climate change to elevate extinction risks.

Modeling approaches

Modeling approach also affected extinction risk estimates. For example, species-area relationship models consistently estimated higher risks than did other approaches (27.4%; CI_{95} : 16.7, 41.7%). Species-area-relationship models extrapolate habitat loss to predict total species extinctions on the basis of empirical relationships between habitat area and species diversity (12). Although these models have a positive bias (29), they also estimate risks for the many rare species with small ranges that are excluded by other approaches owing to insufficient data (30). Therefore, it remains uncertain whether these models are under- or overestimating extinction risks.

Expert analyses also predicted higher extinction risks (14.6%; CI_{95} : 9.8, 21.7%). This category includes both traditional expert analyses and newer climate change vulnerability assessments, which combine projections from species distribution models with expert judgements of species-specific vulnerability and adaptability (31). These assessments might project higher risks either because they embody a more comprehensive expert-driven understanding of species-specific vulnerability and adaptability or because their qualitative extinction thresholds overestimate risks relative to the quantitative thresholds from other approaches.

The remaining models vary along a continuum from fully correlative to fully mechanistic approaches, with a range of intervening hybrid combinations. Although mechanistic models dominated early approaches, they were subsumed by easy-to-use correlative species distribution models during the 2000s (Fig. 4). These approaches associate species' current ranges with current climate variation and extrapolate these associations to project future distributions under different climate change scenarios (32). These models composed >80% of the studies in the meta-analysis, and unsurprisingly, their median risk matched the overall meta-analysis median.

More recently, hybrid and mechanistic approaches have rebounded in prevalence. Today, more models integrate multiple, more sophisticated biological processes (Fig. 4). Hybrid

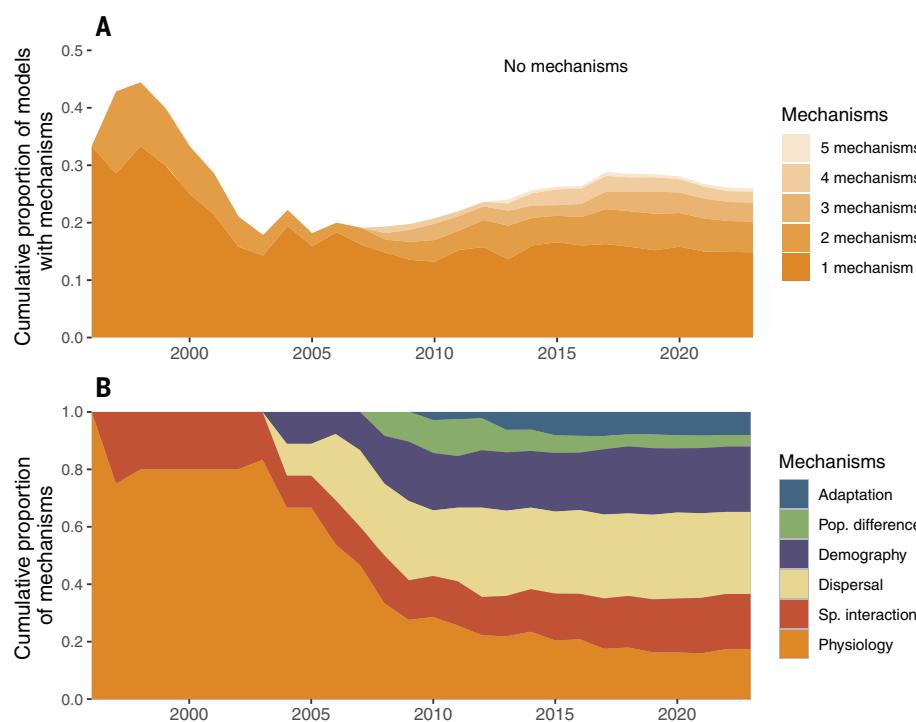


Fig. 4. Climate change extinction models include more mechanisms and more diverse mechanisms.

(A) The cumulative proportion of models with multiple mechanisms (orange shading) has grown through time. (B) More types of mechanisms are included in recent models, including adaptation and population differences.

approaches modify species distribution projections on the basis of biological knowledge, such as by limiting range expansion through species-specific dispersal (33). At the other extreme, fully mechanistic models project extinctions independent of current distributions by using information such as measured physiological thermal limits or climate-dependent demographic variables (34). Mechanistic models projected somewhat lower risks than that of other methods (4.1%; CI_{95} : 2.8, 5.9%), whereas hybrid models returned results similar to those of species distribution models and the global median (7.1 versus 7.6%). Mechanistic models might project lower risks because they have most often been applied to lower-risk northern regions (fig. S34) or the data that are needed to parameterize these more sophisticated models are restricted to better-studied, common species, which generally experience lower risks (7).

Mechanisms

Early hybrid and mechanistic models included physiology, species interactions, and taxaspecific dispersal, whereas recent models have begun to incorporate demography, population differences, and adaptive evolution (Fig. 4B). The mechanisms incorporated into modeling approaches affected extinction risk estimates. Models that included demography and species interactions projected higher extinction risks of 13.2% (CI_{95} : 9.6, 18.1%) and 13.1% (CI_{95} : 9.6,

17.6%), respectively, whereas estimates for other mechanisms matched the median. Demographic models might estimate higher extinction risks because they often translate habitat declines into steeper, nonlinear declines in population abundances, thus exceeding extinction thresholds faster than models of habitat change (35). Species interactions can enhance climate change extinction risks, for example, by introducing new enemies or competitors or reducing the abundances or range overlap for interdependent species such as mutualists or specialized grazers and plants (36, 37). A review found that most observed local extirpations were attributed to species interactions, suggesting that the indirect effects of climate change are often as severe as the direct effects (38). Other biological mechanisms (physiology, dispersal, adaptation, and population differentiation), Earth system models (such as hydrology), and nonclimate habitat variables matched median risks.

Specific assumptions about dispersal did, however, affect extinction estimates (Fig. 3). Models that assumed no dispersal reported higher risks (11.3%; CI_{95} : 9.7, 13.1%) than those that assumed no dispersal limits (5.9%; CI_{95} : 5.1, 6.8%). Dispersal models with taxaspecific dispersal limits, dispersal constrained to contiguous habitats, and fixed intermediate limits did not vary from the overall median. These approaches are useful, however, because they like-

ly predict species-specific responses and risks more accurately (5).

Observed climate change extinctions

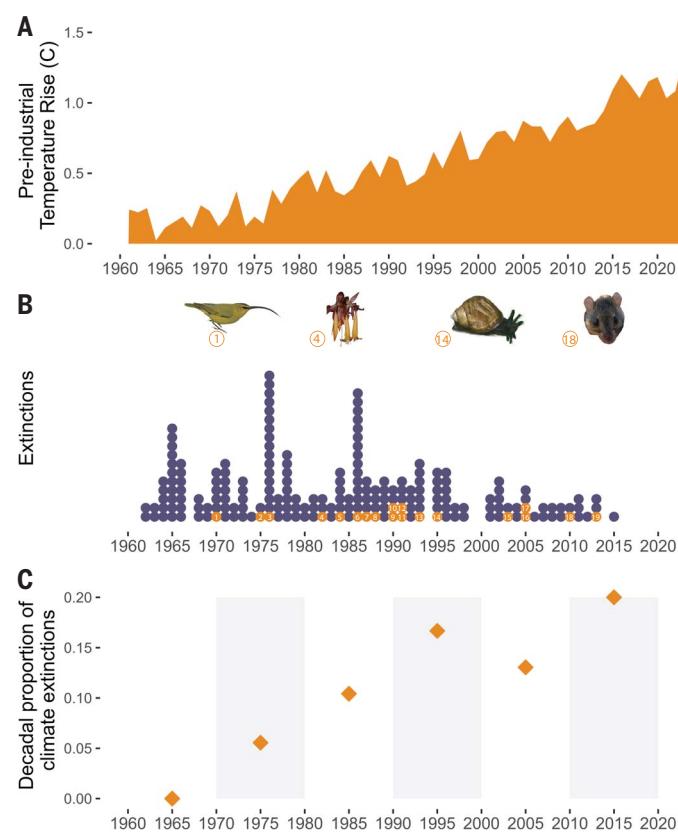
Since temperatures rose above the preindustrial average in the 1960s (Fig. 5A), 19 extinctions have been attributed, at least in part, to climate change (Fig. 5B) (methods, species, confidence levels, and threat attributes are provided in table S6 and supplementary text). The proportion of extinctions attributed to climate change increased 4% per decade [logistic regression slope = 0.79; CI_{95} : 0.02, 1.63] (Fig. 5C). These losses include the Fort Ross weevil and the Bramble Cay melomys, both of which likely became extinct through climate-mediated sea level rise (39); Hawaiian birds affected when warmer temperatures expanded avian malaria to higher elevations (40); and amphibians that became infected with introduced Chytridiomycosis through an uncertain link to climate change (41). Most of these climate change-associated extinctions involved species from island, mountain, and freshwater ecosystems (table S6), supporting this study's findings about these ecosystems' elevated risks (Fig. 3). Yet for most of these extinctions, climate change played an uncertain, interactive, subordinate, and sometimes controversial role relative to traditional threats such as habitat loss and invasive species (42). Unlike other threats, however, climate change can infiltrate the most pristine habitats, negating the effectiveness of protected areas (40, 41). Probabilistic attributions of extinction to climate change are rare, but developing such techniques will be critically important for understanding the contributions of climate change to future extinctions (43). Climate change is predicted to play an increasing and more certain role in causing extinctions in the coming decades.

At current warming levels of $\sim 1.3^{\circ}\text{C}$, 1.6% of species are projected to be threatened with extinction from climate change, translating into 160,000 species, assuming 10 million total species. Yet only 19 extinctions have been recorded and attributed partially to climate change so far. However, recorded extinctions are strongly biased toward vertebrates and underestimate true extinction numbers. Additional species have been lost, including those never discovered or described. Moreover, this discrepancy is expected because of the long-recognized lag time between threat impact and extinction called the "extinction debt" (44). Although changes in greenhouse gases rapidly alter climate patterns, biological responses proceed on a longer and more uncertain schedule. Extinction debts require from years to millennia to pay, depending on species' current abundance, range size, and life history traits (45).

The good news is that these time lags provide a buffer for some species, during which time

Fig. 5. Extinctions attributed in part to climate change. (A)

The global land and sea temperature anomaly in degrees Celsius relative to the 1850–1900 average from NOAA. **(B)** Each dot indicates an extinction and its estimated year from the International Union for Conservation of Nature and Natural Resources (IUCN) Red List. Those extinctions attributed in part to climate change are highlighted in orange. Numbers correspond to table S6 entries. Pictures show the extinct (1) Kaua'i Akialoa honeycreeper, (4) Golden Fuchsia plant, (14) *Pachnodus velutinus* land snail, and (15) Bramble Cay Melomys rat. **(C)** Over time, the proportion of extinctions with a climate change contribution per decade increases. The fewer total extinctions observed recently likely reflect time lags in documenting extinctions. [Photo credits are provided in the supplementary materials.]



climate change might reverse, species might adapt, or conservation efforts might succeed. The bad news is that extinction debts cannot usually be predicted accurately. Improved understanding and better predictive models will be needed to develop a triage approach for determining which species face imminent extinction, which ones would benefit from long-term conservation efforts, and which species face no immediate danger.

Conclusions

Our understanding of climate change extinctions has grown dramatically in the past decade through expansive modeling efforts that span more diverse species and regions and adopt more advanced and realistic approaches. These improvements support a consistent extinction risk from climate change with greater certainty. This consistency may result because adding biological complexity to models can both enhance or diminish predicted climate change impacts, leading to better estimates for individual species but producing an overall balance in global extinction risks. For example, although adding species interactions and demography can increase predicted risk levels, modeling higher dispersal distances for some species

can reduce predicted risks (Fig. 3). Despite increasing certainty, the many unidentified and rare species are usually not modeled because of insufficient data, even though they likely face greater-than-average threats (30). Hence, the estimates presented here represent a lower bound on climate change extinctions, an estimate likely to be surpassed as Earth's hidden biodiversity becomes revealed.

The increased certainty of predicted climate change extinctions compels action. Policy choices among different future scenarios will lead to drastically different outcomes for biodiversity (Fig. 1B). Adopting emissions policies that reduce maximum temperatures from 5.4°C under the SSP 5-8.5 scenario to the SSP 2-4.5 scenario, which is consistent with current commitments, reduces extinction risk from 30 to 5%. But even losing 5% of species would be harmful, if not catastrophic, for biodiversity, ecosystems, and the people that rely on them. Consequently, this study supports the 1.5°C threshold, which would keep extinction threats below 2%. Extinction represents just the final endpoint of a species' existence; even when extinction is avoided, declining abundances and shrinking ranges can strongly affect many other species, including humans. Conserva-

tion efforts must be mobilized to protect the most threatened species with the most immediate extinction debts, as identified by improving predictive models. On the basis of current information, these species will often be amphibians; inhabit freshwater, island, or mountainous ecosystems; be poor dispersers; have small ranges or already be threatened; and most likely will live in South America, Australia, and New Zealand.

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SUPPLEMENTARY MATERIALS

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 Materials and Methods
 Supplementary Text
 Figs. S1 to S39
 Tables S1 to S7
 References (47–580)
 MDAR Reproducibility Checklist

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