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REVIEW

How many species will Earth lose to climate change?

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Abstract

Climate change may be an important threat to global biodiversity, potentially leading to the extinction of numerous species. But how many? There have been various attempts to answer this question, sometimes yielding strikingly different estimates. Here, we review these estimates, assess their disagreements and methodology, and explore how we might reach better estimates. Large-scale studies have estimated the extinction of ~1% of sampled species up to ~70%, even when using the same approach (species distribution models; SDMs). Nevertheless, worst-case estimates often converge near 20%–30% species loss, and many differences shrink when using similar assumptions. We perform a new review of recent SDM studies, which show ~17% loss of species to climate change under worst-case scenarios. However, this review shows that many SDM studies are biased by excluding the most vulnerable species (those known from few localities), which may lead to underestimating global species loss. Conversely, our analyses of recent climate change responses show that a fundamental assumption of SDM studies, that species' climatic niches do not change over time, may be frequently violated. For example, we find mean rates of positive thermal niche change across species of ~0.02°C/year. Yet, these rates may still be slower than projected climate change by ~3–4 fold. Finally, we explore how global extinction levels can be estimated by combining group-specific estimates of species loss with recent group-specific projections of global species richness (including cryptic insect species). These preliminary estimates tentatively forecast climate-related extinction of 14%–32% of macroscopic species in the next ~50 years, potentially including 3–6 million (or more) animal and plant species, even under intermediate climate change scenarios.

KEYWORDS
biodiversity, climate change, cryptic species, dispersal, extinction, global warming, niche shift, species richness

1 | INTRODUCTION

Is anthropogenic climate change an important threat to global biodiversity? If the answer is yes, then climate change will presumably drive many species to extinction within the next 50–100 years, either by itself or in combination with other factors. Yet, the number of species that are at risk from climate change remains highly unclear (e.g., Bellard et al., 2012; Thomas et al., 2004; Urban, 2015). For example, a recent analysis estimated that relatively few species would go extinct across ~120,000 analyzed species of terrestrial plants and animals (Warren et al., 2018), whereas other studies have projected that ~35% of terrestrial plants and animals might go extinct under worst-case climate scenarios (Román-Palacios & Wiens, 2020; Thomas et al., 2004). In 2019, a United Nations report (IPBES, 2019) made headlines when it suggested that a million species could soon go extinct from human impacts, a startling number. But this might be a dramatic underestimate or an overestimate.

The goal of this review is to make sense of these disparate estimates of global extinction from climate change. First, we review several previous analyses of these projected extinctions, many of which were based on species distribution modeling (SDM). Second, we present a new review of recent SDM studies. Third, we describe potential biases in SDM studies and how they might influence these estimates. Fourth, we address the ability of species to rapidly shift their climatic niches, which may be essential for species survival. Finally, we explore how we might better estimate species loss from climate change, with preliminary analyses that combine niche change, dispersal, and recent projections of global biodiversity. For simplicity, we emphasize worst-case climate change scenarios (i.e., upper bounds of species loss), to make estimates more comparable across studies. Extinction projections should converge to low numbers and small differences under best-case scenarios. Unfortunately, more pessimistic scenarios (>2.5°C increase) should be considered given the latest report of the United Nations Environment Programme (2023). Extreme scenarios (e.g., ~4°C increase) may remain likely, especially in the near term (Schwalm et al., 2020; contra Hausfather & Peters, 2020).

We recognize that there have been many previous reviews on the potential impact of climate change on biodiversity (e.g., Bellard et al., 2012; Pereira et al., 2010; Pinsky et al., 2022). Our review differs from others by combining a new review of individual SDM studies, new estimates of rates of climatic niche change, and by integrating taxon-specific forecasts of species loss with recently developed projections of global biodiversity.

We think that biodiversity loss from climate change is an urgent and important topic. Nevertheless, species loss is only one of many potential impacts of climate change, and others are also important (e.g., reductions in ecosystem function; Grimm et al., 2013). Similarly, climate change is only one among many current threats to biodiversity, but one that may be especially hard to protect species from.

2 | WHAT EXTINCTION LEVELS HAVE PREVIOUS STUDIES ESTIMATED?

We present here a brief, chronological review of several prominent studies that have addressed species-level extinction from climate change (Figure 1; Table 1). This list is not comprehensive, but focuses on selected studies that were global in scale (i.e., multiple continents) and spanned major taxonomic groups (e.g., both plants and animals). We review both the proportion of species-level extinctions they projected and how they arrived at these predictions.

In a classic study, Thomas et al. (2004) used projections of future geographic ranges for 1103 animal and plant species for the year 2050 to estimate species loss. These projections were based on SDM, which takes the current climatic conditions where species occur and projects where those conditions will occur in the future. These authors combined these SDM projections (from earlier studies) with estimates of extinction based on species–area relationships (Rosenzweig, 1995). They then estimated the proportion of species that would be "committed to extinction" by 2050 given their reduced (projected) geographic range sizes. "Committed to extinction" means that these species are predicted to go extinct, but not necessarily by 2050. They estimated that, under scenarios of low, intermediate, and high climate warming (increases of 0.8–1.7, 1.8–2.0, and >2.0°C, respectively), a total of ~18%, ~24%, or ~35% of the sampled species would be committed to extinction by 2050.

Malcolm et al. (2006) analyzed 25 biodiversity hotspots and estimated the loss of endemic species based on how much the biomes in

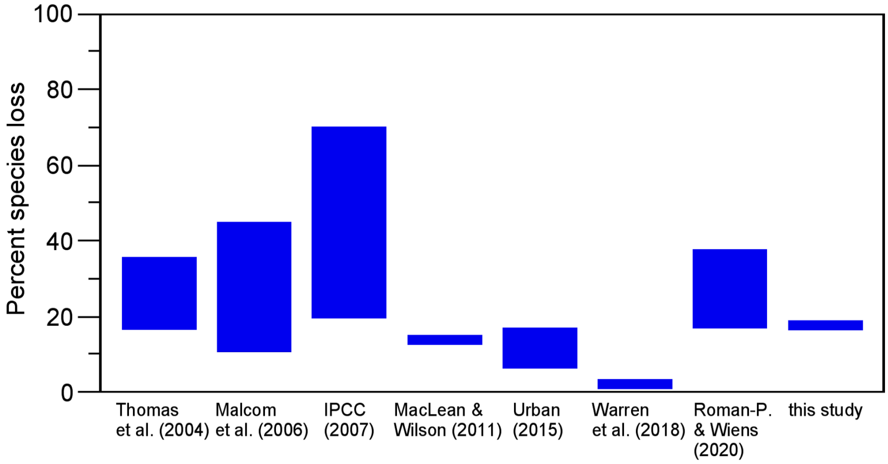

FIGURE 1 Summary of projections of species loss from climate change. For each study we give the percentage of all the sampled species that were projected to go extinct because of climate change. Most studies assumed that species will go extinct when 100% of their geographic ranges become climatically unsuitable, based on species distribution modeling. Further information on each study is given in Table 1. Many studies gave a range of estimates across different climate-change scenarios, and these are presented as a solid bar spanning the highest and lowest of their main estimates. The highest estimates generally correspond to the RCP 8.5 scenario with a ~4°C increase, except for Thomas et al. (2004; >2°C increase), Malcolm et al. (2006; not specified) and MacLean and Wilson (2011; not specified). For "this study" we present our own estimates of the percentage of species projected to go extinct, based on recent studies using species distribution modeling (Dataset S1).

TABLE 1 Summary of projected extinction from climate change.

Study	Organisms	Overall estimate	Worst case
Thomas et al. (2004)	1103 plants, animals	18%–35%	35%
Malcolm et al. (2006)	133,149 plants, 9645 vertebrates	11.6%	43%
IPCC (2007)	Plants, animals	20%–30%	40%–70%
MacLean and Wilson (2011)	305 plants, animals, fungi, protists	14%	—
Urban (2015)	>560,000 plants, animals	7.9%	15.7% (~40%)
Warren et al. (2018)	119,968 plants, animals	<5%	—
Román-Palacios and Wiens (2020)	538 plants, animals	16%–30%	30%–35% (35%–42%)
This study	400,169 mostly plants, animals	—	16.9%

Note: We give the study, the organisms included (number of species and major taxonomic groups), the overall estimate of the percentage of species projected to go extinct from climate change (across climate-change scenarios), and the percentage estimated under a worst-case scenario (RCP 8.5; ~4°C increase in global mean annual temperatures). The number in parentheses for the worst-case scenario for Urban (2015) is the estimate when dispersal is not allowed or if species-level extinction is inferred based on >80% range loss. The number in parentheses for the worst-case scenario for Román-Palacios and Wiens (2020) is the estimate when extinction rates are inferred using the increase in maximum temperatures at which 50% of populations go extinct instead of 95%. "This study" refers to our summary of SDM studies from 2015 to 2022.

each hotspot would be reduced in area under climate change (in the next ~100 years). A total of 133,149 endemic plant species and 9645 endemic vertebrate species were included. They estimated that between 1% and 43% of species would be lost overall, depending on various factors, such as species' migration abilities and how specific each species is to the biome(s) where it occurs. They estimated loss of 11.6% of these species after averaging across scenarios and factors.

In 2007, the IPCC estimated 20%–30% loss of species by 2100 under climate change scenarios with a 2–3°C increase in mean annual temperatures relative to pre-industrial levels (Fischlin et al., 2007, p. 242; also referred to here as IPCC 2007). For an increase >4°C, they suggested a range of 40%–70%. These estimates were described as being derived mostly from Thomas et al. (2004), Malcolm et al. (2006), and from their own review of the literature (their table 4.1). However, they did not describe a methodology for obtaining overall estimates of species loss from individual studies.

MacLean and Wilson (2011) estimated species extinction risk by 2100 based on responses to climate change (e.g., population declines) from 305 marine and terrestrial taxa, including plants, animals, fungi, and protists. Their predictions yielded a 14% probability of extinction across species, but they did not address specific climate change scenarios.

In one of the most influential recent studies in this area, Urban (2015) compiled projections of climate-related species extinctions from 131 published studies. These studies collectively spanned >500,000 species (but with some overlap of species among studies). Most studies ($n=107$) used SDM to project species' future geographic ranges. The overall estimate was that 7.9% of the included species would go extinct due to climate change (by 2020–2106, but mostly 2050–2100). This overall estimate assumed intermediate dispersal anywhere and that species would not go extinct unless >95% of their original habitats became climatically unsuitable. Under the most extreme climate change scenario (representative concentration pathway [RCP] 8.5; ~4°C increase in global annual mean temperature), the overall estimate was 15.7% extinction. Furthermore, there were variations on this scenario with ~40% extinction, such as when no dispersal was allowed, or if species were considered "committed to extinction" if they lost >80% of their climatically suitable habitats. Under more moderate climate change scenarios (e.g., 2°C increase), extinction was correspondingly lower (5.2%).

Warren et al. (2018) used an SDM approach to project climate change impacts on 119,968 terrestrial species by 2100 (expanding on Warren et al., 2013). These species consisted of plants (73,224 species), invertebrates (34,104; with 31,536 insects), and chordates (12,640). They projected that under high levels of warming (RCP 8.5; ~4°C increase) many species would lose >50% of their geographic ranges, including 67% of plants, 68% of invertebrates, and 44% of chordates (given realistic dispersal rates; their table S2). Furthermore, the total projected range loss across species was 59% in plants, 57% in invertebrates, and 34% in chordates (given realistic dispersal; their table S3). However, they estimated that very few species would have their entire geographic ranges become climatically unsuitable (<5% of plant species, and fewer in animals), and most species would retain >20% of their geographic range area. SDM analyses can be unreliable when based on few data points, and Warren et al. (2018) therefore excluded species represented by <10 distinct geographic localities. Warren et al. (2013) noted that excluding species with smaller range sizes could bias extinction estimates by excluding small-ranged species that are potentially the most vulnerable. We return to this idea below.

Román-Palacios and Wiens (2020) projected species-level extinctions for 2070 based on rates of dispersal and local extinction for 538 plant and animal species. Rather than using SDM, they estimated dispersal and local extinction based on published surveys and resurveys along elevational transects over time (including only native species and only transects where habitat modification was not a potential explanation for local extinction). They found that 44% of these species had already gone locally extinct at the hottest sites on these transects and that local extinctions were best predicted by increases in maximum annual temperatures. They projected that species would go extinct if maximum temperatures throughout their ranges (after dispersal) increased to levels beyond which populations typically went extinct (based on logistic regression). Under an extreme climate change scenario (RCP 8.5; ~4°C increase), they projected extinction of ~30%–35% of these species, at least along these transects. Under more moderate scenarios (RCP 4.5; ~2°C increase), extinction was correspondingly lower (~16%).

Overall, these studies suggest a relatively broad range of possible species losses (Figure 1), even when using similar methods (e.g., SDM). For example, the extensive analyses by Warren et al. (2018) suggest little or no species loss even under the most extreme climate scenario (RCP 8.5), whereas IPCC (2007) estimated from 40% to 70%. Nevertheless, for the worst-case climate scenario (RCP 8.5), many estimates converge near ~20%–30% (Malcolm et al., 2006; Román-Palacios & Wiens, 2020; Thomas et al., 2004; Urban, 2015) and especially ~20% (Figure 1; Table 1).

There are many other important studies of climate change responses not listed here. We summarize these briefly in Table 2, and at greater length in Appendix S1.

3 | NEW SDM REVIEW AND ESTIMATE

We conducted a new review of studies that predicted extinction from climate change, subsequent to those reviewed by Urban (2015). This review was intended as a complement to that review, and an opportunity to address potential methodological issues. The details are given in Appendix S2. We obtained information from 82 studies that collectively included projections for 400,169 species (Dataset S1). Many projections were from large-scale analyses of plants (368,050 species; Di Marco et al., 2019), freshwater fish (16,662 species; Manjarrés-Hernández et al., 2021), and birds (8268 species; Stewart et al., 2022). There was some taxonomic overlap among species (e.g., one study included all plant species, but there were also many smaller-scale studies of plants). Yet, there were at least 392,980 non-overlapping species (>98.2%).

To make estimates comparable across studies, we focused on the most pessimistic climatic scenarios (i.e., RCP 8.5; ~4°C increase in mean annual temperature). Almost all studies were based on SDM. Most studies included dispersal, such that species could move to adjacent areas that were climatically suitable. Here, we followed the standard approach in SDM studies and considered a species as projected to go extinct if none of its projected current or future geographic range would be climatically suitable in the most distant year considered (typically 2050–2100).

Given these specifications, a total of 67,660 species out of 400,169 were projected to go extinct (16.9%). This number is very similar to the comparable estimate by Urban (2015) for RCP 8.5, which is 15.7% (see their fig. 2). There was no consistent impact of the date of the future projection (i.e., most studies used 2050, 2070, 2080, or 2100, with extinction of 15.7%, 39.7%, 7.5%, and 4.8% of species, respectively; Dataset S1).

TABLE 2 Studies on climate change that were not included.

Study	Summary
Foden et al. (2013)	Estimated relative climate vulnerability among 16,857 animal species, including amphibians (6204), birds (9856), and corals (797)
Newbold (2018)	Used SDM= for birds, mammals, amphibians, and non-avian reptiles to analyze climate change impacts for 20,392 species. Estimated loss of 37.9% of species from local communities under RCP 8.5 by 2070
IPBES report (2019)	Estimated that ~25% of plant and animal species and 1 million species in total were threatened with extinction (but not necessarily by climate change or climate change alone)
Trisos et al. (2020)	Suggested that by 2100, 81% of terrestrial assemblages and 37% of marine assemblages would have species exposed to annual mean temperatures outside their historical temperature ranges
Manes et al. (2021)	Based on a meta-analysis of data from biodiversity hotspots, they concluded that under high climate change scenarios (increase of >3°C), 34% of endemic species in terrestrial ecosystems and 46% in marine ecosystems would be at high risk of extinction from climate change
Strona and Bradshaw (2022)	Used simulations to analyze local-scale changes in tetrapod diversity from 21,143 species. Estimated local loss of 40%–50% of species in tropics
Boyce et al. (2022)	Analyzed climatic vulnerability of 24,975 marine species
Murali et al. (2023)	Analyzed future exposure of species to extreme heat in future climates, based on data from 33,548 species of land vertebrates
Pigot et al. (2023)	Analyzed future exposure of species to maximum climatic temperatures outside their historical range for 31,790 terrestrial species (all vertebrates) and 4073 diverse marine species

Note: For each study we give a brief summary. Most of these studies did not directly estimate future species-level extinctions. One study did estimate extinctions (IPBES, 2019) but did not clarify how many of those extinctions were related to climate change. Studies are listed chronologically. Further details for each study are listed in Appendix S1, including an explanation for why they were not included in Table 1. Note that this is not a comprehensive list, and only some of the most prominent studies are listed.

4 | WHY DO SOME SDM STUDIES GIVE SUCH DIFFERENT ESTIMATES?

A major motivation for this review is the observation that different studies can give very different projections of species extinction from climate change. How do we make sense of these differences? Most studies used the same general approach (SDM), which makes these differences even harder to understand.

First, different studies may use different scenarios of future climate change. Broad-scale studies agree that more species will likely go extinct if future temperatures are higher (e.g., Thomas et al., 2004; Urban, 2015). However, projections can also differ strongly under similar future climate scenarios. For example, under the most extreme climate-change scenarios, Thomas et al. (2004) suggested that ~35% of sampled species would go extinct, whereas Urban (2015) estimated roughly half that (~16%). Therefore, other factors must be involved.

Second, studies have used different criteria for forecasting species extinction. SDM studies often project that some portion of a species' current geographic range will become climatically unsuitable. Many studies projected that a species would go extinct only when 100% of their geographic range became unsuitable. But a species might instead be considered "committed to extinction" if it is projected to lose >95% or even >80% of its range area. Urban (2015; fig. S2) showed that given a pessimistic climate change scenario (~4°C increase), ~10% of the sampled species would go extinct using a threshold of 100% range loss, whereas ~30% would be committed to extinction using a threshold of 80% (helping to bring some divergent estimates into closer agreement). Similarly, the large-scale SDM results of Warren et al. (2018) indicated that few species would have their entire ranges become unsuitable, but Parmesan et al. (2022) used those results to show that under a pessimistic climate change scenario (~4.5°C increase) there was "very high" risk of extinction (>80% range loss) for ~15% of plants, fungi, and chordates, and ~25% of invertebrates. It is unclear what threshold should be used. For example, a species with a small initial range size may not survive losing 80% of it, whereas this loss may not drive species-level extinction if the initial range size was large. Beyond the loss of area alone, it may also be important if the remaining climatically suitable habitats are isolated from each other and whether each one can support enough individuals to maintain viable populations. Some studies have used species–area relationships to project how the loss of climatically suitable range area will influence species survival (Thomas et al., 2004). Urban (2015) found that studies based on species–area relationships projected extinction levels that were roughly twice those based on SDMs alone. This could help reconcile the two-fold difference in comparable extinction projections between Thomas et al. (2004) and Urban (2015). There has also been debate about the use of species–area relationships for estimating extinction (e.g., He & Hubbell, 2011; Thomas & Williamson, 2012).

Different assumptions about dispersal can also influence these estimates. If it is assumed that species cannot disperse to new areas, then if their current geographic range becomes climatically unsuitable, they are generally projected to go extinct. However, if they can disperse, there is potential for them to track suitable climatic conditions to new areas adjacent to their current geographic range. Many SDM studies explore the impact of dispersal on their projections of species survival. Many others assume that species will be able to disperse quickly enough to find new locations. Nevertheless, numerous studies project species-level extinctions even when dispersal is allowed. This occurs when no suitable climates are projected to remain in the region where a species occurs. Incorporating restrictions on dispersal can also help bring disparate climate estimates into closer agreement (e.g., Thomas et al., 2004; Urban, 2015; see above).

5 | ARE SDM STUDIES OF CLIMATE-RELATED EXTINCTION UNBIASED AND RELIABLE?

There are several general sources of bias in studies of climate change impacts based on SDM. Different factors can bias studies for or against inferring future species-level extinction. There is a large literature on this topic (e.g., Nadeau et al., 2017; Peterson et al., 2018; Zurell et al., 2023), but we briefly highlight some key biases here.

A widespread but infrequently discussed bias is that SDM studies often exclude species with few localities, in order to ensure that models yield accurate results. Yet these excluded species may be those most threatened by climate change. Specifically, those species with the fewest localities will typically have small geographic range areas (i.e., limited area of occupancy and extent of occurrence; Gaston & Fuller, 2009). Therefore they will be more likely to go extinct as parts of their ranges become unsuitable (Pearson et al., 2014). This range size bias has been mentioned (e.g., Warren et al., 2013; Zurell et al., 2023), but not in many of the most prominent and well-cited SDM-based studies (e.g., Thomas et al., 2004; Urban, 2015; Warren et al., 2018). Furthermore, to our knowledge, it has not been quantified.

How common is this source of bias? In our review of SDM analyses published from 2015 to 2022 (Dataset S1), studies reported excluding (on average) 28.2% of the relevant species because these species had too few localities ($n=55$ studies reported this information). The other 27 studies (32.9%) did not explain the overall completeness of their taxonomic sampling. Furthermore, 33 of these 82 studies (40.2%) mentioned excluding species with too few localities or that were otherwise rare, even if they did not give quantitative criteria.

Conversely, some studies focus on a single region and its endemic species and so may be biased against including broadly distributed species that may be more resilient to range loss from climate change (e.g., Manes et al., 2021). The solution to both sources of bias is to perform broad-scale studies that are as taxonomically comprehensive as possible (within the group of interest).

Several other limitations of SDM have also been discussed. SDM methods generally assume that the climatic variables determining a species' current geographic range will determine their future distributions (Pearson & Dawson, 2003). But climate-related extinction might be caused by climatic factors different from those setting their current range limits. Furthermore, future climates may be novel relative to current climates, potentially making spatial predictions based on current climates inaccurate in the future (e.g., Williams & Jackson, 2007).

Similarly, species may not occur in all the climatic conditions that they can tolerate (e.g., because of species interactions, geographic barriers, habitat destruction, overharvesting, or other factors). This issue has been referred to as "niche truncation" (Bush et al., 2018; Peterson et al., 2018). Niche truncation may cause SDM to underestimate where species could occur in the future, and overestimate extinction (e.g., Faurby & Araújo, 2018). Nevertheless, broad-scale syntheses of transplant experiments suggest that range limits frequently concur with niche limits (Hargreaves et al., 2014; Lee-Yaw et al., 2016).

More broadly, it remains unclear whether SDM studies give accurate projections of extinction under climate change. Some authors have compared predicted and observed changes in species distributions among temperate birds over several decades, finding that SDM either did (Araújo et al., 2005) or did not (Sofaer et al., 2018) provide accurate predictions. Hijmans and Graham (2006) considered some SDM approaches to be accurate, based on comparison to mechanistic models based on physiology alone from 100 plant species.

Other authors have used the congruence between climatic distributions in species' native and introduced ranges to evaluate whether niches are stable enough over time to allow SDM to predict future distributions (Guisan et al., 2014). These analyses have yielded mixed results, with some studies finding similar realized climatic niches between the native and introduced parts of species' ranges (e.g., Liu, Wolter, et al., 2020; Petitpierre et al., 2012) and others finding them to be dissimilar (e.g., Atwater et al., 2018). Beyond introduced species, SDM studies assume that species climatic niches will not change substantially over time (Pearson & Dawson, 2003). We address this issue in the next section.

In summary, we have highlighted a widespread source of bias in broad-scale SDM studies of global extinction from climate change: species are preferentially selected that may be the least vulnerable (i.e., known from more localities, and thus more common and/or more widely distributed). More generally, the accuracy of SDM for predicting future climate change impacts remains disturbingly unclear: the relevant studies have been limited in scope and in conflict, such as the analyses of temperate birds over time (Araújo et al., 2005; Sofaer et al., 2018) and niche change in introduced plants (Atwater et al., 2018; Petitpierre et al., 2012). We question whether SDM should be considered to generate the most reliable estimates of future extinction simply because there are so many of these estimates across species (Table 1).

6 | CAN NICHE CHANGE KEEP PACE WITH CLIMATE CHANGE?

A widespread assumption in many approaches to estimating climate change impacts is that if species are exposed to conditions outside their current climatic niches, they will likely go extinct (Tables 1 and 2). From first principles, we know that if species cannot disperse quickly enough to remain within their original climatic niche, then their survival will depend on shifting their niches to accommodate the new climatic conditions (Holt, 1990). Can species' climatic niches change as fast as climate will?

This question has been addressed in various ways (Figure 2; Table 3). One way is to look at the rate of niche change among populations and species that diverged thousands or millions of years ago, using phylogeny-based approaches (e.g., Jezkova & Wiens, 2016; Quintero & Wiens, 2013). These analyses suggest that niche change is thousands (if not millions) of times slower than the projected rate of modern climate change (Figure 2; Table 3). These results potentially justify the assumption of little or no niche change over time in SDM studies. Yet niche change is averaged over very long timescales

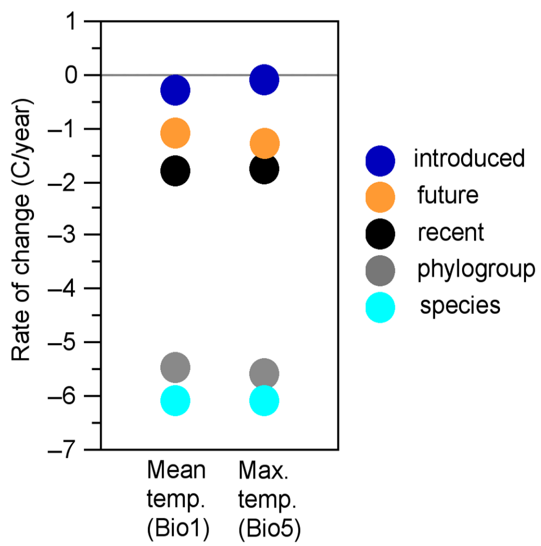

FIGURE 2 Comparing estimated rates of climate change and climatic niche change for temperature-related variables. Rates are mean values across species and are shown on a log10 scale. Details of these rate estimates are given in Table 3, along with estimates for precipitation. In short, the estimates from introduced species are based on comparing the climatic niches of native and non-native populations of a limited number of vertebrate species ($n=5$ and 12 for Bio1 and Bio5, respectively). Estimates for "future" are based on projections of the rate of future climate change across the geographic ranges of 1265 terrestrial vertebrate species. "Recent" estimates are based on surveys of plant and animal populations over time, from 538 species, using the positive niche shifts (Table 3). "Phylogroup" estimates are from phylogeny-based analyses of 266 groups of populations (identified from phylogeographic analyses) from 56 plant and animal species. "Species" estimates are from phylogeny-based analyses of 2087 species of plants and animals. Methodological details are given in Appendix S3.

TABLE 3 Comparing different estimates of rates of niche change and rates of climate change.

	Mean temp. (Bio1)	Max. Temp. (Bio5)	Precip. (Bio12)
Recent niche change			
Overall mean (*n*=538 species)	−0.0145°C/yr ±0.0027	−0.0158°C/yr ±0.0026	1.0367 mm/yr ±0.2234
Mean positive	0.0171 (*n*=348) ±0.0011	0.0179 (*n*=277) ±0.0014	2.7746 (*n*=385) ±0.2241
Mean negative	−0.0724 (*n*=190) ±0.0050	−0.0516 (*n*=261) ±0.0041	−3.3363 (*n*=153) ±0.3532
Future climate change (*n*=1265 species)	0.073°C/yr ±0.0014	0.048°C/yr ±0.0010	7.969 mm/yr ±0.2207
Introduced species (*n*=5–33 species)	0.539°C/yr (*n*=5) ±0.366	0.857°C/yr (*n*=12) ±0.382	118.996 mm/yr (*n*=33) ±38.043
Among populations (*n*=266 populations)	3.6°C/Myr ±0.612	2.8°C/Myr ±0.373	344 mm/Myr ±52.22
Among species (*n*=2087 species)	1.105°C/Myr ±0.0721	1.073°C/Myr ±0.0618	171.874 mm/Myr ±14.7708

Note: Each value is a mean among species (or populations) followed by the standard error of the mean. We give further details for how rates are calculated in Appendix S3. The rates compared here include: (1) rates of recent niche change, estimated here based on changes at species' warmest-edge localities on elevational transects over decadal timescales, (2) projected future climate change (from geographic ranges of terrestrial vertebrate species; Quintero & Wiens, 2013), (3) changes between native and introduced populations of terrestrial vertebrate species (Wiens et al., 2019), (4) changes among plant and animal populations (phylogroups) from within-species, time-calibrated phylogenies (Jezkova & Wiens, 2016), and (5) changes among plant and animal species inferred from species-level phylogenies (Liu, Ye, & Wiens, 2020). Note that rates for recent niche change and introduced species are in units of change per year (yr), whereas those among populations and among species are in change per million years (Myr).

in these cases, which may underestimate rates over the shorter, decadal timescales relevant to climate change (e.g., Gingerich, 2009).

Analyses in introduced vertebrates (over decadal timescales) suggest a very different pattern (Wiens et al., 2019): that some introduced species can shift their realized climatic niches even faster than rates of projected climate change, by roughly tenfold (Figure 2; Table 3). These dramatic niche shifts were sometimes associated with the initial introduction of these species to the non-native range, making them effectively instantaneous. Thus, these climatic conditions must have already been within the species' climatic tolerances. These rapid shifts occurred despite an overall relationship between climatic conditions in the native and introduced ranges among these species (meaning that such relationships do not rule out rapid change). However, it is unclear whether introduced species offer a reasonable proxy for how native species might respond to changing climate. For example, niche shifts may be constrained in these species' native ranges by their interactions with other species (Wiens et al., 2019), and not all species may be capable of such rapid niche shifts.

There is now a way to address the rate of warming-related niche change that is more direct than using phylogenetic trees or introduced species. One can analyze climatic niche change in response to climate change in recent decades, by combining surveys of species distributions over time with climatic data from each time period (Figure 3). We illustrate this approach here, using published distributional (Table S1) and climatic data for 538 species (Román-Palacios & Wiens, 2020). Further methodological details are given in Appendix S3, and relevant estimates and data for each site and species are given in Datasets S2–S4. We emphasize that these resurveys over time are a well-established approach for examining recent impacts of climate change (e.g., Chen et al., 2011; Lenoir et al., 2020; Moritz et al., 2008; Parmesan, 2006; Riddell et al., 2021; Rumpf et al., 2019; Sinervo et al., 2010). In short, we think that the best way to predict responses to future climate change is by analyzing responses to climate change in the very recent past.

For a given species (Figure 3), we utilized localities on elevational transects that were surveyed at two timepoints (e.g., 1970s vs. 2010s), based on data from 10 resurvey studies (Table S1). There was an average of 41.2 years between surveys, and 58.1 localities per transect. We used climatic data for each site from the time period of each survey, based on empirical mode decomposition (EMD; Huang et al., 1998), a standard approach for capturing long-term trends and reducing the effects of year-to-year climate variability. In alternative analyses, we used climatic data based on the mean of a 5-year window before each survey, and a 10-year window. We focused on three climatic variables: annual mean temperature (Bio1), maximum temperature of the warmest month (Bio5), and annual precipitation (Bio12). Maximum temperature may be an especially important driver of local extinction (Román-Palacios & Wiens, 2020). We did not perform multivariate analyses given our interest in rates for individual climatic variables, and the need to compare these rate estimates to others for the same variables (Figure 2; Table 3).

For a given climatic variable (Figure 3), we estimated the climatic niche shift as the difference between the niche limit (value at the hottest site) at the time of the initial survey and the niche limit at the time of the resurvey (value at the hottest site, even if the hottest site is different). The rate of change is the niche shift divided by the time between surveys.

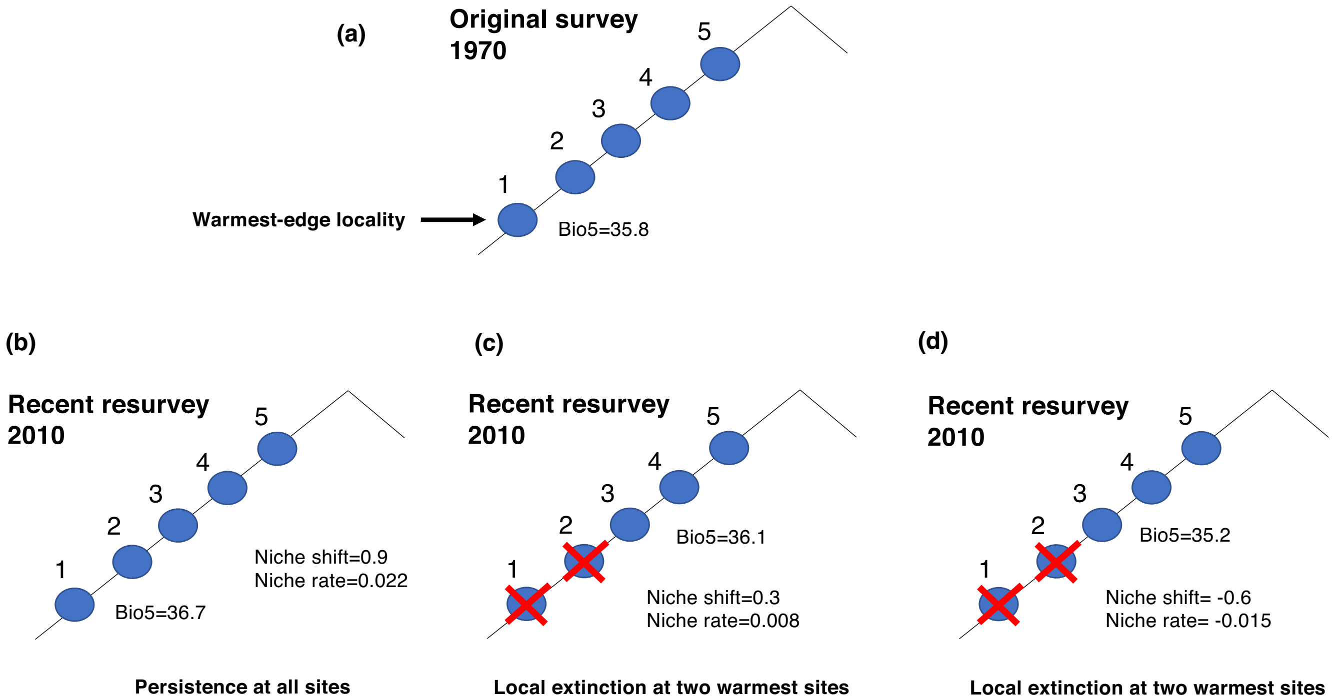

FIGURE 3 Estimating rates of niche change based on recent responses to climate change. In this hypothetical example, a given species has been surveyed at five sites along an elevational transect at two time periods (1970 and 2010). (a) In 1970, the species occurred at five surveyed sites along the transect. The maximum temperature of the warmest month (Bio5) was 35.8°C at the warmest (lowest elevation) of these sites. We illustrate three possible scenarios for these sites after they were resurveyed in 2010. (b) In the first scenario, the species persisted at all five sites. The warmest-edge site increased in Bio5 by 0.9°C. This is the magnitude of the niche shift, and the rate is the shift divided by the time between surveys (40 years). (c) In the second and third scenarios, the species went locally extinct at the two warmest sites (sites 1 and 2) between surveys. Here, the niche shift is estimated based on the 2010 value of Bio5 at the warmest site where the species still occurs (site 3). In the second scenario (c), site 3 in 2010 is warmer than site 1 was in 1970. Therefore, there is a positive niche shift of 0.3°C. (d) In the third scenario, site 3 in 2010 is cooler than site 1 was in 1970. Therefore, there is an apparent negative climatic niche shift in Bio5 (the warmest-edge site is cooler than it was previously).

These niche shifts (and rates) for temperature variables could have positive or negative values (Figure 3). For example, the species might still persist at the hottest locality where it initially occurred on the transect (i.e., lowest elevation). In this case, the species niche limit will shift positively, toward hotter temperatures as climate warms (Figure 3b). Alternatively, the species could go extinct at that initial hottest site, and might now occur at a site that was initially cooler (e.g., at a higher elevation). This new range edge might now be warmer than the old range edge, again leading to a positive niche shift (Figure 3c). If the new lowest elevation site is still cooler than the previous niche limit even after climate change, then the warm-edge niche shift will be negative (Figure 3d). For annual precipitation, a negative niche shift may simply indicate decreasing precipitation between surveys.

We estimated niche rates for 538 species. These included 132 plant species and 406 animal species. Most sampled animals were insects ($n=267$), whereas the rest were vertebrates ($n=139$, 78% birds, but also including amphibians and squamate reptiles). The majority of the species were tropical ($n=347$). Overall, this sampling reflects some of the major large-scale diversity patterns (i.e., more tropical than temperate species, more animals than plants, more insects than vertebrates), but is not perfectly proportional or representative of all groups or regions (Appendix S3).

These 538 species showed both positive and negative changes in their temperature-related niche variables (Table 3). For both mean and maximum temperatures, positive changes (shifts to warmer temperatures) occurred at a rate of ~0.02°C/year, whereas negative changes were ~2–3 times faster than the positive changes. Rates of niche change were generally similar using the mean climatic values from across localities at each time point, not just the niche limits (Table S2; Dataset S4). These results based on mean niche values demonstrate that the rates based on niche limits are not simply artifacts associated with using only the single warmest-edge locality for each species. These rates of climate change were only weakly (and negatively) related to rates of niche change for this variable ($r^2=.016$; $p=.0030$; $n=538$ species). This is a non-phylogenetic regression, but incorporating phylogeny (if available), would primarily impact p-values, since the regression should be unbiased (Rohlf, 2006). Mean rates were generally similar between animals and plants and between tropical and temperate species (Appendix S3) and the overall mean rates (Table 3) were most similar to mean rates from animals and from tropical species.

The mean rates of positive niche change among these species were slower than mean projections of the pace of future climate change, by 4.2 times for mean temperature and 2.7 times for maximum temperature (Table 3). The overall rate for annual precipitation was 7.7 times slower than projected change in this variable (Table 3). Thus, the answer to our initial question here (can niche change keep pace with projected climate change?) seems to be: close, but not generally fast enough.

Rates of niche change associated with recent climate change were slower than those from introduced species and much faster than those from phylogenetic analyses of populations and species (Figure 2; Table 3). Relative to the recent rates estimated here, rates for introduced species into warmer climates were about 31.5 times faster than recent positive shifts for annual mean temperature and 47.9 times faster than recent positive shifts for maximum temperatures (and 42.9 times faster for recent shifts into wetter climates). Conversely, mean rates of recent niche change were thousands of times faster than rates among populations (phylogroups) from phylogenetic analyses (~5000–8000 times faster; for positive rates). Rates among species were even slower than those among populations, by roughly threefold to fourfold (Table 3). These results show that niches can change substantially over the decadal timescale of recent climate change.

Another way of looking at these results is to compare the extent of these niche shifts to each species' original niche width on these transects (Table 4; Appendix S3). For example, species' recent niche shifts are (on average) >25% of their original niche widths for mean and maximum temperatures, for both positive and negative niche shifts.

Some species persisted even when there was no overlap between their current and previous climatic conditions for this variable. For example, for mean and maximum temperatures, 15.6% and 9.8% of the species showed no overlap between their current and former climatic niche (84 and 53 of 538 species; Dataset S2). Although this may seem surprising, it is not unprecedented. For example, among 76 introduced vertebrate species, 10.5% showed no overlap with their native ranges for maximum temperatures (Wiens et al., 2019).

Species with negative niche shifts (Table 4) lost more of their ranges than expected based on the change in these climatic variables alone: if range loss perfectly matched climate change, then the niche shift would be effectively zero. These results suggest that species' current climatic conditions (and species-distribution models based on them) can underestimate how much change species can tolerate, but might also underestimate their vulnerability in some cases. Other potential explanations for this pattern are given in Appendix S3.

Rates were higher using the 5-year and 10-year windows to estimate climatic values for each timepoint (Datasets S5–S8) instead of EMD. The rate of positive niche change (Table S3) was 0.06–0.10°C/year for mean annual temperature ($n=372$–373 species) and 0.05–0.06°C/year for maximum temperature ($n=372$–374 species). The mean rates of positive niche change outpaced future climate change (Table 3) for maximum temperatures, but the overall mean rates of niche change remained slower for all three variables (Bio1 = 1.8–15.5-fold slower; Bio5 = 2.7–4.1-fold; Bio12 = 15–233-fold). Patterns were similar using mean values among localities (Table S4; Datasets S9 and S10). Mean proportional overlap was generally >0.5 for both positive and negative niche shifts (Table S5; Datasets S5 and S6).

Overall, the many positive niche shifts inferred here indicate that many populations and species can tolerate climatic conditions outside of those where they initially occurred. Yet, there are also limits to the changes that many species can tolerate, given that 44% of these 538 species had local extinction at their warmest sampled site (similarly, an analysis of 976 species showed warm-edge local extinctions in 47%; Wiens, 2016). Logistic regression analyses inferred that 50% of these warm-edge populations would go extinct when exposed to an increase in maximum temperatures of 0.519°C (Román-Palacios & Wiens, 2020). Among the 538 species, 162 species had an increase in hottest temperatures (Bio5) of 0.530°C or more at their warmest site. Among these 162 species, 97 went locally extinct at this site (59.9%). No species were exposed to an increase >1.187°C or a rate of climate change faster than 0.079°C/year. Logistic regression analyses suggested that 95% of the species would go extinct if all their populations were exposed to increases in maximum temperatures >2.860°C.

In summary, these analyses suggest that it may be problematic to infer that species will go extinct based on SDM studies that assume no niche shifts are possible. Similarly, it would also be problematic to (hypothetically) infer extinction of a species based solely on their exposure to temperatures outside their current climatic means (Trisos

TABLE 4 Proportional overlap between niche shifts and the species' original niche width.

	Mean annual temp. (Bio1)	Maximum temp. (Bio5)	Annual precip. (Bio12)
Overall mean	0.010 ($n=477$) ±0.0243	−0.107 ($n=477$) ±0.0224	0.383 ($n=477$) ±0.0307
Mean positive	0.344 ($n=299$) ±0.0174	0.274 ($n=232$) ±0.0211	0.741 ($n=345$) ±0.0167
Mean negative	−0.555 ($n=178$) ±0.0233	−0.471 ($n=245$) ±0.0198	−0.554 ($n=132$) ±0.0348

Note: Each value is a mean among species followed by the standard error of the mean. These overlaps were estimated based on species that were surveyed on elevational transects over decadal timescales. The details of calculating these mean proportional overlaps are described in Appendix S3. A total of 61 species were excluded because they occurred at a single locality on a transect, making it impossible to calculate the range of values across sites.

et al., 2020) or maxima (Murali et al., 2023). These analyses here, although limited, show that many species have responded to recent climate change by substantially shifting their climatic niches. Indeed, some species now occur entirely outside their initial climatic niches. Yet, there has also been widespread local extinction among these species, and the widespread negative niche shifts inferred here (Table 3) suggest that SDM analyses might also underestimate local extinction in some cases. These analyses will not be the last word on niche shifts in response to climate change, but they demonstrate how this approach can be applied and some major patterns.

Finally, it is important to note that these analyses are agnostic about the underlying mechanisms. For example, niche shifts could involve evolution of physiological tolerances or could involve plasticity alone (e.g., individuals survive in a warmer climate simply by spending more time in the shade). Similarly, although these analyses do not incorporate detailed mechanisms, they do implicitly take into account the potential effects of biotic interactions, thermoregulation, and microhabitat refuges. Thus, if populations could avoid extinction by (for example) utilizing local microclimate refuges, then they would presumably not have gone locally extinct. Nevertheless, these other factors might help predict which species go locally extinct and which do not in the face of similar levels of climate change. Microhabitat (Riddell et al., 2021) and climatic niche width (Grinder & Wiens, 2023) may be particularly important variables for predicting climate-related local extinctions. Specifically, use of underground microhabitats by desert mammals to escape surface heat helps explain their increased survival relative to birds at the same sites (Riddell et al., 2021). Species with narrower climatic niche widths for temperature (e.g., tropical species) appear to be more vulnerable to local extinction from climate change (Grinder & Wiens, 2023). Additional studies are needed that incorporate niche shifts when projecting species-level extinction, and that incorporate the factors that underlie the variability in climate change responses among species. We also note that various other approaches can be used to estimate niche shifts (e.g., Labisko et al., 2022) and rates of adaptive climate change responses (e.g., Bonnet et al., 2022; Radchuk et al., 2019), without necessarily estimating rates of temperature change per year (as done here).

7 | HOW MANY SPECIES WILL EARTH LOSE TO CLIMATE CHANGE?

Given these many complexities of projecting extinction and survival from future climate change, how do we even start to answer this question? We think that one promising approach (Figure 4) would involve three steps: (1) obtain reasonable projections of the percentage of climate-related extinction from representative species in the most species-rich groups; (2) multiply the percentage of species lost by the group's projected richness to estimate the group's number of species lost; and (3) sum these losses across groups to estimate the overall number of species lost. Importantly, previous estimates of the overall percentage of species lost from climate change (Table 1) have not generally considered how these estimates are impacted by differences among groups in both projected species loss and species richness. Both must be considered (e.g., the overall percentage of species loss should depend far more on the estimate for insects than vertebrates).

We present a preliminary worked example here (Table 5). This is intended to illustrate the overall approach, rather than being a definitive estimate of species loss. We used projections for 2070 from a previous study (Román-Palacios & Wiens, 2020). That study used data on species responses to climate change in recent decades, including the increases in maximum temperatures associated with local extinction and how quickly species dispersed. A species was considered to go extinct when exposed to a potentially extinction-causing increase in maximum temperature throughout its geographic range, after accounting for dispersal. There should be no question about the relevance of these data to extinction from climate change. However, other approaches for estimating extinction could be used in this same framework (Figure 4), including SDM and mechanistic modeling of species ranges (e.g., Kearney & Porter, 2009).

Future climates are often estimated based on a combination of a RCP and a general circulation model (GCM). We initially used the worst-case RCP (RCP 8.5) and the 17 GCMs available for that pathway. We considered a species to go extinct when extinction was projected across >50% of the GCMs. Other details (and potential weaknesses) are given in Appendix S4. The underlying data are given as Datasets S11–S16. The estimates are summarized in Dataset S17. We also provide estimates using an intermediate scenario (RCP 4.5, ~2.5°C increase). The latter estimates are given subsequently, with the underlying data in Datasets S18–S23.

We present estimates of the proportion of species-level extinctions for three important groups: insects, vertebrates, and plants (Table S6). These estimates vary depending mostly on how one estimates the maximum temperature increase thought to drive local extinction (i.e., 50% vs. 95% logistic regression threshold). Different assumptions about dispersal (for species not observed to disperse upwards between surveys; Appendix S4) generally had negligible effects on the projected percentage of species lost (~0%–2%; Table S6). These proportions of species-level extinction can then be combined with the estimated richness of these groups to estimate overall species losses (Figure 4). Importantly, the most information on projected species losses were available from insects ($n = 267$ species, 5 studies; Table S1), with their sampling dominated by tropical species (77.9%; $n = 208$).

Insects are pivotal for estimating global biodiversity (and diversity loss). Insects make up ~50% of all described species across kingdoms (1 of 2 million), and ~67% of animals (Catalogue of Life [COL]; Bánki et al., 2021). Several studies have used diverse methods to estimate the total number of insect species (both described and undescribed), and converged on ~6 million species (Basset et al., 2012; Gaston, 1991; Novotny et al., 2002; Odegaard, 2000; Stork, 2018; Stork et al., 2015). Assuming ~6 million insect species and climate-related extinction of 22.7%–30.7% (RCP 8.5; Table S6), then 1.4–1.8 million would be lost to climate change (Table 5).

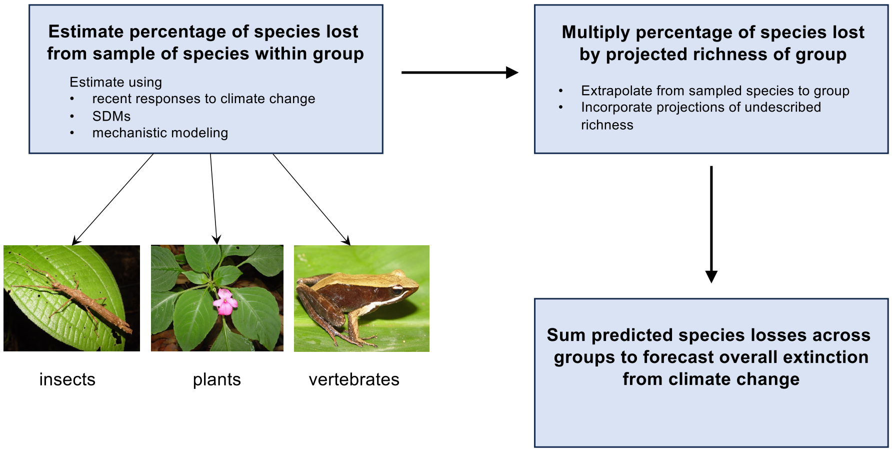

FIGURE 4 General framework proposed here for estimating global species loss from climate change. This framework involves three main steps: (1) obtain reasonable forecasts of the percentage of climate-related extinction from representative species in the most species-rich groups (insects, plants, and vertebrates are illustrated here). These forecasts could come from various approaches, including recent responses to climate change (used here), species-distribution modeling (SDM), and mechanistic modeling. (2) Multiply the estimated percentage of species lost in each group by the group's projected richness (i.e., potentially including both described and projected undescribed species) to estimate the group's total number of species lost. (3) Sum these losses across groups to obtain the overall number of species lost (or the overall percentage of species lost). The results of a preliminary analysis based on this approach are shown in Table 5 (for an extreme climate change scenario, RCP 8.5, ~4°C increase) and Table S8 (for an intermediate climate-change scenario, RCP 4.5, ~2.5°C increase). Note that many previous estimates of the overall percentage of species lost (e.g., Figure 1; Table 1) may be problematic because they did not account for both the different percentages of species potentially lost in each group and the different numbers of species in each group (both will influence the overall percentage of species projected to be lost). Photographs from John J. Wiens.

However, these projections of insect diversity were based on species that were recognized as distinct using morphological characteristics. Recent estimates of morphologically cryptic species based on molecular markers have projected that there are (on average) ~3 cryptic species per morphology-based species (Li & Wiens, 2023). These projections take into account differences in mean numbers of cryptic species among insect orders and seem robust to several potential sources of bias. Incorporating cryptic species leads to an estimate of 21.1 million insect species (assuming 3.11 cryptic species per morphology-based species and 6.8 million morphology-based insect [and related terrestrial arthropods] species; Stork et al., 2015).

Given 21.1 million insect species (and loss of 22.7%–30.7%; Table S6), leads to the projected loss of 4.790–6.477 million of them to climate change. However, these cryptic species might be far more vulnerable to climate change than morphology-based species. Cryptic species presumably have smaller geographic range sizes than other species, since each typically occupies a fraction of the geographic range of the morphology-based species they were initially assigned to (Bickford et al., 2007; Larsen et al., 2017). Species with smaller range sizes may be especially vulnerable to climate change (Pearson et al., 2014). Therefore, loss of 4.8–6.5 million insect species to climate change may be an underestimate.

These estimates are just for insects, but most other macroscopic groups may be unlikely to substantially alter these very large numbers. For example, plants are estimated to include ~320,000–360,000 species in total (Joppa et al., 2011; Mora et al., 2011). The current number of described plant species is 378,239 (COL; March 23, 2023), but including some algae. Roughly 86,995–117,254 plant species might be lost, considering 378,239 species and loss of 23%–31% (Table 5). For chordates, current richness is 73,502 species (COL; March 23, 2023) but we do not know of estimates that are dramatically larger (~80,000 by Chapman, 2009). Our estimates for land vertebrates suggest 35%–44% species loss, and total loss of 26,461–32,341 species. Note that even if the projections of species loss for plants and vertebrates were drastically incorrect, there would be little impact on overall extinction estimates, given the numerical dominance of insects. Similarly, even given many cryptic chordate and plant species, these would have limited impact on overall losses. Furthermore, large-scale analyses in mammals suggest limited cryptic diversity in vertebrates relative to insects (e.g., mean of <1 cryptic species per morphology-based species; Parsons et al., 2022). We do not know of evidence for large numbers of cryptic species in plants. Therefore, our initial estimate for animals and plants combined is ~5–6 million species lost under pessimistic climate scenarios (RCP 8.5; ~4°C increase; Table 5). Under more moderate scenarios (RCP 4.5; ~2.5°C; Tables S7 and S8), the estimate is ~3–6 million species (Table S8; Dataset S24).

At least four other major groups should be considered: (1) microscopic organisms (e.g., bacteria, archaeans, protists); (2) fungi; (3) marine animals; (4) animals associated with insect hosts (e.g., mites and nematodes). We discuss each in more detail in Appendix S4. In short, extinction estimates comparable to those used for insects, plants, and terrestrial vertebrates are lacking for these groups. We therefore excluded microbes and utilized workarounds for the others (Appendix S4; Table 5). Importantly, insect-associated animals might number 60 million species or more. Assuming that these would go extinct if their insect hosts did (Table S6), then Earth could lose 20 million animal species or more (Table 5).

TABLE 5 Estimates of potential species loss from climate change, including both described and projected species.

Group	Described species	Projected species	Percent extinction	Described species lost	Total species lost
Plants	378,239	378,239	23%–31%	86,995–117,254	86,995–117,254
Insects	972,539	21.1 million	23%–31%	223,684–301,487	4.8–6.5 million
Vertebrates	73,502	73,502	36%–44%	26,461–32,341	26,461–32,341
Marine animals	187,890	0.7–2.1 (1.0) million	3%–87%	5637–163,464	30,000–870,000
Insect-associated animals	<44,000	63.5 million	23%–31%	10,120–13,640	14.6–19.7 million
Fungi	154,538	6.3 million	23%–31%	33,998–47,907	1.449–1.953 million
Total	1,810,708	92.352 million		386,895–676,093 (21.4–37.3%)	20.992–29.172 million (22.7–31.6%)

Note: For each group, we give the number of known (described) species, projected species numbers (described and undescribed), percentage of species projected to be lost under a high-emission climate scenario (RCP 8.5), number of described species projected to be lost, and the total number of species projected to be lost. Percentages of species lost are from Table S6 for plants, insects, and vertebrates (ranges are for the 50% and 95% thresholds from logistic regression, averaged across three dispersal scenarios). For plants and vertebrates, numbers of described and undescribed species are relatively similar, and we used the number of described species for both. For described insect species, we used an estimate from the Catalogue of Life (June 10, 2023; Bánki et al., 2021). For other groups, we describe the estimates of species numbers and species lost in Appendix S4. We used 1 million marine animal species (Appendix S4). Estimates using an intermediate climate scenario (RCP 4.5) are given in Table S8.

We appreciate that some readers may be uncomfortable with these estimates, because the species that are projected to be lost are merely hypothetical. Yet, the IPBES (2019) estimate of 1 million species lost also assumed many millions of undescribed species (following Mora et al., 2011). Furthermore, projections of smaller species numbers can have their own strong assumptions. For example, there is now evidence for numerous cryptic species among morphology-based species in the largest insect orders (Li & Wiens, 2023). Assuming an average of three cryptic species per morphology-based species may seem like a strong assumption, but assuming a mean of 0 instead is contrary to dozens of studies.

Another important assumption of these analyses is that undescribed species will be just as likely to go extinct as described species. For vertebrates, more recently described species tend to be narrowly distributed, tropical, and threatened (Liu et al., 2022; Moura & Jetz, 2021). This pattern may apply to undescribed insects as well. Small range size and tropicality may both make species especially vulnerable to climate change (Grinder & Wiens, 2023; Manes et al., 2021; Pearson et al., 2014; Xu et al., 2023). On the other hand, more narrowly distributed, undescribed species might be less likely to contain cryptic species, which might lower overall estimates of insect diversity (and loss). Yet, tropical and temperate insects seem to contain similar numbers of cryptic species (Li & Wiens, 2023). Clearly, this is an area in need of further study.

The proportional estimates of extinction here are similar to some previous ones based on SDM (Figure 1; e.g., IPCC, 2007; Thomas et al., 2004) but are larger than others (e.g., Urban, 2015; Warren et al., 2018). Yet, as described above, these different SDM estimates can converge when including species-area effects or limited dispersal (Urban, 2015). Thus, our overall estimates here are not radically different from previous ones. But these previous large-scale SDM studies (Figure 1) did not correct for differences in species richness among groups, even among described species. Note that estimating the overall percentage of species that will be lost to climate change hinges on both the estimated number of species in each group and the percentage projected to go extinct. Thus, estimating the overall percentage of species lost across groups is not more conservative than estimating absolute numbers of species lost: they both depend on the same numbers.

8 | CAVEATS AND FUTURE RESEARCH

We have presented preliminary estimates of climate-related species loss that take into account patterns of global biodiversity among groups and recent impacts of climate change (Figure 4; Table 5). These analyses hinge on many assumptions, which is why we consider them preliminary. We mention two assumptions here, but additional ones are given above and in Appendices S3 and S4. First, we assume that projections based on resurveys of elevational transects provide a reasonable approximation of species-level extinction. Species survival will ultimately depend on rates of extinction, niche change, and dispersal. These rate estimates are not perfect, but they should not necessarily be biased for or against extinction by sampling few transects per species. The same applies to the density of sampling localities along each transect. Nevertheless, further study would be valuable. We emphasize that resampling transects is a well-established approach for documenting climate change impacts (e.g., Chen et al., 2011; Lenoir et al., 2020; Moritz et al., 2008; Rumpf et al., 2019; Sinervo et al., 2010).

Second, the sampling of species from these recent climate change studies is limited ($n = 538$), and does not include all groups in all regions (Appendix S4). By contrast, the SDM approach has now generated estimates for hundreds of thousands of species. But whether SDM results accurately predict climate-related extinction remains unclear and largely untested (see above). Furthermore, SDM studies are often biased by excluding the likely most vulnerable species, which seems highly problematic for estimating global biodiversity loss with this approach.

Several types of data and methods are urgently needed. We need more information on these climate change responses (extinction, niche shifts, dispersal) from additional groups and habitats (e.g., bacteria, fungi, freshwater species, marine species), and more species from more regions for plants, insects, and vertebrates. With accelerating climate change, it may now be possible to conduct meaningful resampling studies of extinction, niche change, and dispersal over much shorter timescales (e.g., ~7 years; Holzmann et al., 2023) than before (e.g., ~41 years; Table S1). We also need new methods that can help translate information from these recent climate change responses into better species-wide projections of extinction, dispersal, and survival. Future projections must also account for the greater vulnerability and richness of tropical species.

To better estimate biodiversity loss from climate change, we also need better estimates of biodiversity. Assuming no cryptic species is no longer tenable but current estimates of cryptic insect diversity could be improved. Specifically, we need to estimate how cryptic insect species are distributed among the millions of projected undescribed species, not just among described species. Furthermore, we need to understand how vulnerable these undescribed and cryptic species are to climate change. They are presumably at greater risk given smaller range sizes but this should be quantified and the extinction estimates modified accordingly.

9 | CONCLUSIONS

How many species will be driven to extinction by climate change? Previous studies have sometimes yielded very different estimates of the proportion of species that are in danger. Most studies were based on SDM. Previous and new summaries here often project roughly 20%–30% species loss under worst-case climatic scenarios using this SDM approach. However, these summaries contain at least two important sources of bias: they may underestimate extinction because they generally exclude narrowly distributed species (which are more at risk from climate change) and they may overestimate extinction because they do not incorporate the ability of species to shift their climatic niches. We show here that niche shifts can be relatively rapid and widespread. Nevertheless, niche shifts have been insufficient to prevent local extinction in ~45% of plant and animal species that have been resurveyed over time. Furthermore, mean rates of recent niche change appear to be slower than mean projected climate change for key temperature variables. Therefore, niche shifts may not prevent widespread, species-level extinctions. We illustrate an overall framework for forecasting global-scale species loss, based here on taxon-specific analyses of niche shifts, dispersal, and local extinction that have already occurred, combined with recent taxon-specific projections of global species richness. These preliminary estimates tentatively suggest that Earth may lose ~3–6 million macroscopic species in the coming decades, and possibly many more. We emphasize that to understand how climate change will impact biodiversity in the future, we should incorporate information on how species have already responded to recent climate change. Furthermore, understanding the impacts of climate change on biodiversity will also require a better understanding of biodiversity itself, and especially the number, distribution, and vulnerability of Earth's many undescribed species.

AUTHOR CONTRIBUTIONS

John J. Wiens: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing. **Joseph Zelinka:** Formal analysis; investigation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on figshare as Datasets S1–S24 at https://doi.org/10.6084/m9.figshare.23605692 (Wiens & Zelinka, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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