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Improvements in reports of species redistribution under climate change are required

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Studies have documented climate change–induced shifts in species distributions but uncertainties associated with data and methods are typically unexplored. We reviewed 240 reports of climate-related species-range shifts and classified them based on three criteria. We ask whether observed distributional shifts are compared against random expectations, whether multicausal factors are examined on equal footing, and whether studies provide sufficient documentation to enable replication. We found that only ~12.1% of studies compare distributional shifts across multiple directions, ~1.6% distinguish observed patterns from random expectations, and ~19.66% examine multicausal factors. Last, ~75.5% of studies report sufficient data and results to allow replication. We show that despite gradual improvements over time, there is scope for raising standards in data and methods within reports of climate-change induced shifts in species distribution. Accurate reporting is important because policy responses depend on them. Flawed assessments can fuel criticism and divert scarce resources for biodiversity to competing priorities.

INTRODUCTION

As climate changes, so do species distributions. Evidence is mounting that ongoing climate changes are causing species to redistribute globally (*1*, *2*). The magnitude of distributional shifts is now estimated to be 2.5 times greater than originally thought (*3*). While many studies have uncovered the existence of nonrandom latitudinal or altitudinal shifts in species distributions (*3*–*5*), consistent with the hypothesis that climate change is driving them, others found that shifts can lag behind climate change owing to physiological plasticity, microclimate buffering, and delayed responses (*6*–*8*). These lags can lead to nondetection of ongoing distributional changes and failures to detect the mechanisms underpinning them. Observational studies have also detected species redistributions not following clear climatic gradients (*9*–*11*). These seemingly idiosyncratic responses to climate change could be related to complex interactions among temperature, precipitation (*12*), land-use change (*13*), species climatic tolerances (*14*), and biotic interactions (*15*). Complex nonlinear species responses to climate change can also limit the ability to detect distributional changes. This is particularly true with approaches assuming simple, often linear, relationships between temperature and species distributions (*10*). Measuring range dynamics along spatial gradients, such as latitude or altitude, can also mask complex biological responses to climate change because these gradients are not precise surrogates for temperature gradients, let alone for multiple climate dimensions (*16*, *17*).

Unlike the literature involving modeling of future climate change effects on species distributions, where several studies have examined uncertainties and addressed questions related to the minimum standards that should be required to make statements about modeled patterns (*18*, *19*), there is an unexpected lack of analyses evaluating the quality of observational inferences regarding climate change effects on past species distributions. As a first step toward weighting the strength of the observational evidence provided by these studies, we review the literature involving the analysis of multiple species responses to climate change (see Materials and Methods; fig. S1) in light of three important criteria: (i) pattern detection, which is the ability to discern signal from noise in patterns of species distributional shifts; (ii) causality, which is the ability to attribute climate change as the most plausible driver of observed distributional shifts given alternative mechanisms; and (iii) reproducibility, which is the ability to replicate studies given the information provided.

Each one of these criteria is assessed by a simple "yes" or "no" answer to six questions linked with the three criteria (Table 1). Stronger support to the conclusions in the reviewed studies is expected for those comparing distributional changes across multiple geographical directions, investigating multiple alternative causal mechanisms potentially driving distributional changes, and describing results with enough detail to enable replication and reanalysis.

RESULTS

Using extensive search of the literature (see Materials and Methods), we identified 240 studies examining the effects of climate change on the distributions of multiple species. Existing research is strongly biased toward the Northern Hemisphere (78.9%) and terrestrial ecosystems (80.4%) (Fig. 1A). Specifically, studies predominate in North America and Europe, mainly western Europe and within the United Kingdom, with notable knowledge gaps emerging in South America, Africa, Asia, and the Middle East [see also (*20*)]. We also found that evidence of climate change effects on species distribution has been examined for ≤2% of reptiles, insects, plants, algae, crustacean, and mollusca; 2.9% of mammals; 2.3% of fishes; and 23.47% of bird species (Fig. 1B).

When examining how the different studies characterize the direction of species distributional shifts, we found that only ~12.1% (n = 29)

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Table 1. Checklist used to measure the strength of evidence about species distributional shifts and their link with climate.

Evaluation criteria
Question of interest: Are distributional changes different from that expected in the absence of major external drivers, that is, by chance? ***I. Pattern detection*** ***a.*** Are range changes analyzed simultaneously across all possible directions of change? Yes = 1, No = 0 ***b.*** If so, are the obtained results compared against a null model expectation enabling distinguishing the observed patterns from chance expectation? Yes = 1, No = 0
Question of interest: Are potential causal factors rather than temperature examined in equal footing? ***II. Attribution*** ***a.*** Are explanatory causes of range changes investigated? Yes = 1, No = 0 ***b.*** If so, are alternative causal explanations compared on equal footing? Yes = 1, No = 0
Question of interest: Are distributional changes described with sufficient details to enable replication and reanalysis of the results? ***III. Reproducibility*** **a.** Are results presented for each individual species? Yes = 1, No = 0 ***b.*** If not, is variation among range dynamics of different sets of species described? Yes = 1, No = 0

compare shifts simultaneously across all possible geographical directions (*21*–*23*). That is, they generally investigate the species range changes across the expected direction of climate change (typically temperature change) while ignoring comparison with distributional changes across alternative directions (Fig. 2, A and B). Of the 29 studies that examine distributional changes across multiple directions, just four tested whether observed distribution shifts could have arisen by chance by comparison with a suitable null model (*8*, *24*–*26*). Analyses of species distributional shifts across multiple directions were mostly conducted with animals (n = 25). Plants feature in just four assessments (*27*–*30*). Unlike studies addressing distributional changes in a single dimension (e.g., latitude or altitude), studies examining range shifts in multiple directions typically found shifts to be idiosyncratic while being difficult to ascribe a clear direction of change [e.g., (*12*, *31*, *32*)].

When investigating links between species distributions and climate change, ~59% (n = 142) of the studies explicitly examine how temperature change covaries with species distributional changes. However, most studies disregard other environmental drivers, such as precipitation change, land-use change, or the interactions among them. Of the reviewed studies investigating the causes of distribution shifts other than temperature change (36.4%; n = 87), only 19.66% (n = 47) have tested alternative causal factors on equal footing (Fig. 2A). Complex interactions among temperature and precipitation change, and species-specific tolerances intervening on species responses to climate changes, were examined in a few studies so far [e.g., (*10*, *33*)].

When examining the reproducibility of studies, we found that ~25.5% (n = 59) did not report data at the individual species level; a requirement for full reanalysis and replication of the studies (Fig. 2A).

The degree to which studies met our criteria also varied among regions: Australia, northern Europe, and a few studies in North America were generally more proficient (Fig. 2, B and C). For example, among 40 papers that received a score of 4 in our criteria scoring, 42.5% (n = 17) are in Europe and 37.5% (n = 15) are in North America. In total, only 6 studies of 240 received a score of 5, in which two of them are in Europe, three of them in North America, and one in Africa. Great Britain, although with the highest number of species distributional change studies (n = 37), had an average (median) of just two subcriteria met. China with three studies reviewed averaged three subcriteria met (*34*–*36*), all reporting heterogeneous and diverse responses of species to climate change (Fig. 2, B and C).

Overall, studies performed poorly against the three criteria (six subcriteria) used (see Table 1). Of the 240 papers reviewed, only 11 (4.5%) met the three criteria, i.e., detected changes in all possible directions, considered at least one other causal factors rather than temperature, and presented the results for individual species meeting all the three main criteria (Fig. 3). Just 16.6% (n = 40) met four subcriteria, and only 2.5% (n = 6) met five subcriteria [e.g., (*23*, *34*)]. In general, studies conducted for terrestrial ecosystems achieved greater performance according to the subcriteria used (Fig. 2B), although the sample size of studies in terrestrial ecosystems (n = 193; 80.4%) is much larger than in marine ones (n = 47).

We analyzed how the different aspects reflecting the quality of studies evolved through time given the criteria. We found that the studies' performances had a tendency to increase across all criteria (Fig. 4). For example, among studies that measured multidirectionality of range shifts (n = 29), 26 were published from 2011 onward. Likewise, in this period, 60 of 87 studies investigated multiple causal factors, while 116 of 181 met our criteria for reproducibility.

DISCUSSION

Species adapt to changes in climate by moving to more suitable locations (*37*). Alternatively, some species might be able to persist throughout their known distributions because of phenotypic plasticity or adaptive genetic modification (*38*, *39*). When neither of these options are available, species perish (*40*). The combined adaptive responses of species to climate change leads to changes in species ranges. Detecting changes using fragmented samples of data and identifying potential causes for those changes is particularly challenging.

There are considerable uncertainties regarding the speed of distributional shifts (*41*–*43*), particularly along rear (contracting) edges (*44*, *45*), the accelerating or mitigating effects of biotic interactions (*46*, *47*), the capacity to adapt in situ associated with expressions of phenotypic plasticity (*38*, *39*) or genetic modification (*48*), and the effects of interactions among multiple climate drivers of change (*49*). The tolerances of species to climate extremes are generally inferred with statistical approaches (*50*–*52*). However, circumstantial evidence suggests that inferred tolerances are narrower than real ones (*15*, *53*). Combined, these biological and environmental effects can truncate the pace and direction of biological responses to climate change. Delayed responses are common (*54*), resilience to changes (*55*) has been observed, and the unknown consequences of novel climates are hard to anticipate (*56*).

In addition, current estimates of climate change effects on species distributions are severely hampered by geographic and taxonomic biases in the underlying data [Fig. 1; see also (*20*)]. Most data come from species-poor, mostly temperate, regions. In sharp contrast, the tropics hosting the vast majority the planet's biological diversity (*57*) scarcely have any study assessing climate change effects on species. A range of factors affects the availability of biodiversity-related information. The knowledge gap in tropics, for example, is related to insufficient funding, inadequate infrastructure, and scarce local

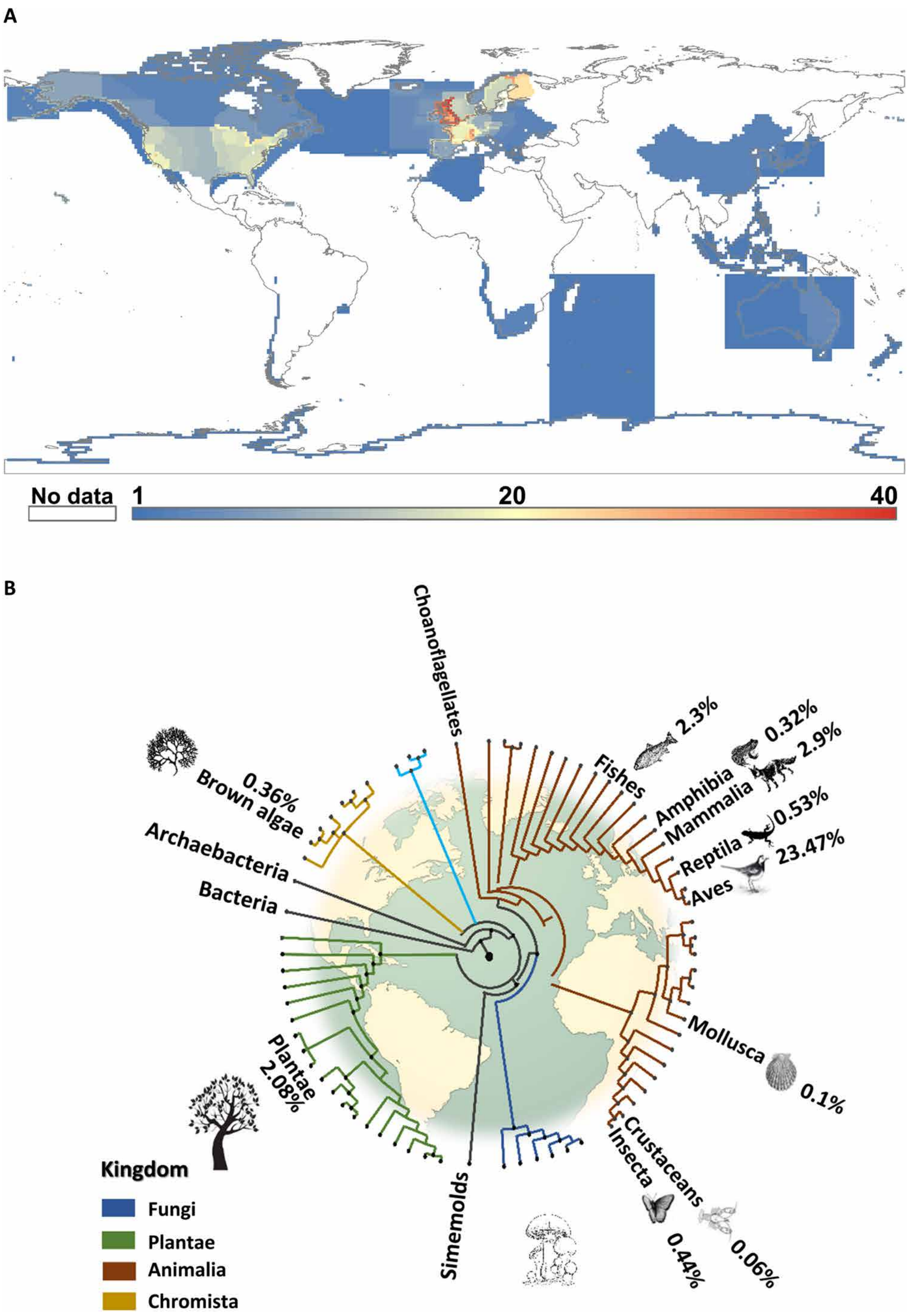

Fig. 1. Geographic and taxonomic coverage of climate related range shifts studies. (**A**) Geographical coverage across terrestrial and marine realms with 82% of the studies being in the Northern Hemisphere while 80.4% covering terrestrial ecosystems. (**B**) Taxonomic coverage with ≤2% including studies with amphibians, insects, reptiles, algae, crustaceans, and mollusca; 2.3% including fish; 2.9% mammals; and 23.47% birds.

expertise for data collection and identification, inaccessibility to research sites because of the political upheaval, and difficulties in getting data published or public (*58*). In addition, geopolitics (*59*), regional democracy (*60*), socioeconomic, history, culture, scientific interest (*61*), and unwillingness of sharing the data play an important role in biodiversity data collections and publishing bias.

While the impact of climate change on the future of biodiversity has been assessed for a wide range of taxonomic groups, the total number of empirical studies remains relatively low. One important reason for this is the lack of replicable historical surveys [but see (*62*)] that limit the reliability of the assessed empirical relationships between species distributional changes and environmental changes (*63*).

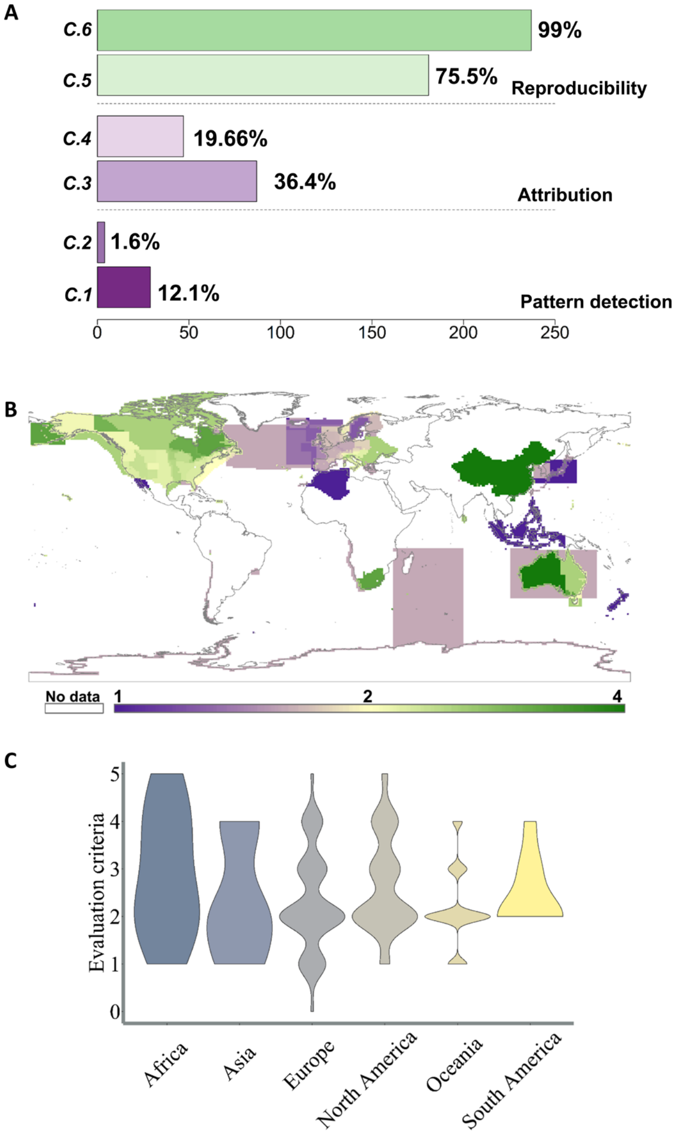

Fig. 2. The quality assessment in climate-related range shifts reports. (**A**) The proportion of reports for six subcriteria. The plot shows the proportion of each study met each criterion (C.1 and C.2, pattern detection; C.3 and C.4, attribution; and C.5 and C.6, reproducibility). (**B**) Assessed quality of the reports of species redistribution under climate change across marine and terrestrial ecosystems. Shows the geographical distribution of studies investigating climate change effects on species distributions ranked by the overall (median) benchmark score achieved through summation of individual ranks in the three evaluation criteria. Values in the map range from 1 (only one of the evaluation subcriteria met) to 4 (four of the evaluation subcriteria met). Higher scores are colored green and lower scores are colored violet. (**C**) Sum of the evaluation subcriteria in each continent. Shows the number of evaluation subcriteria met by each study across continents.

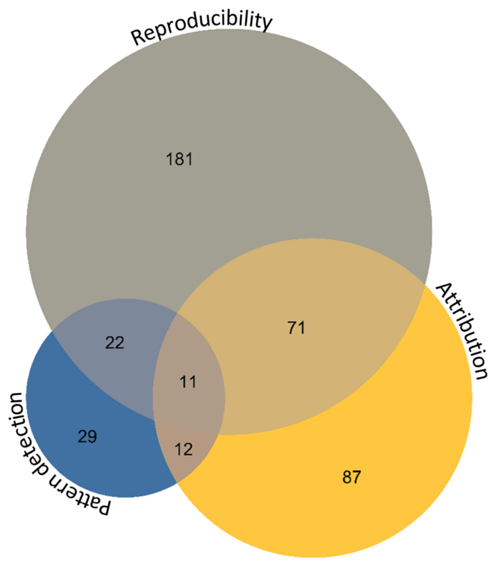

Fig. 3. Cross-examination of the subcriteria used to evaluate reports of species redistribution under climate change. Shows the multiple overlapping among the three main criteria. Each circle corresponds to one of the main evaluation criteria. The size of the circles represents the number of reports met each main criterion (pattern detection, causality, and reproducibility). The Reuleaux triangle in the center shows the intersection between three circles, and it means only 4.5% ($n = 11$) of the studies met these three main criteria.

Studied clades also represent an extremely small fraction of the world's life forms: insects, by far the most specious group in the world, are almost not covered by assessments, and most studies are based on trees and vertebrates with 23% conducted on birds alone. Any conclusion drawn from existing data is thereby regional, taxonomically biased, and hardly transferable globally. Possible generalizations are, therefore, limited.

Adding to the limitations of the data, we found that most studies underperform on the methodological standards of analysis. These are, however, more easily circumvented than the limitations of data. To ascertain whether a distributional shift occurs in response to a given environmental driver, one needs to assess changes not only along the expected gradient but also along alternative gradients (*22*). That is, if species are expected to change along a south to north gradient, for example, then one needs to measure whether the changes along latitude are significantly different from the changes along longitude. If not, then it will be difficult to ascertain that changes are not a consequence of natural population dynamics of range expansion and contraction (*64*). Even when distributional changes are examined across multiple directions, one might still ask if observed patterns could not have arisen by chance given geometrical constrains for dispersal or alternative environmental driver dynamics (*26*). Addressing these questions requires the use of null models of distributional change, but although null models have made their way into ecology (*65*, *66*) and biogeography (*67*), they are still hard to find in studies of climate change effects on biodiversity.

That correlation does not imply that causation is well known. Nevertheless, when a good mechanistic hypothesis exists linking a pattern and the potential underlying mechanisms, and when expected relationships are observed repeatedly across different regions and times, accumulation of evidence can be interpreted as supporting hypothesized causal links between pattern and mechanism (*18*). This is the logic linking elevation and latitudinal shifts with climate change: As temperature increases, higher latitudes and elevations are expected to warm, hence receiving more warm tolerant species while losing cold tolerant ones. Such is an observation dating as far as the classic observations of A. von Humboldt in the Chimborazo Mountain of Ecuador (*62*, *68*). However, climatic gradients do not always follow geographical gradients linearly (*12*), and most often there are

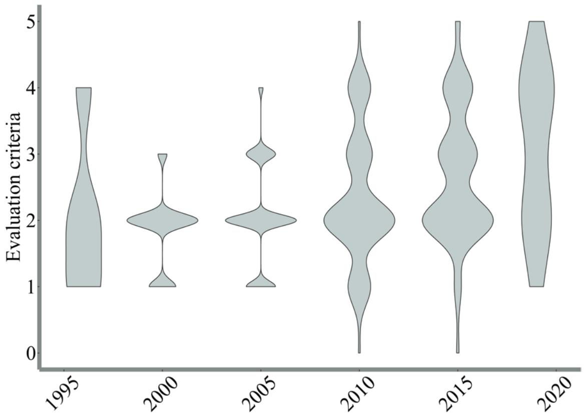

Fig. 4. Distribution of studies by evaluation subcriteria over time. Shows a general trend of improvement of reports of climate-related range shifts over time across the six subcriteria. Higher values in the *y* axis mean that more of the established evaluation criteria were met.

feedbacks between temperature and other climatic variables (e.g., humidity and wind) that further affect the expected relationship between temperature and geographic gradients (*69*). Seeking to attribute climate change to a given distributional shift is thus better achieved by relating species range changes with climate variables instead of geographical proxies, such as latitude and elevation. This point has been made several times for studies examining diversity gradients along elevation gradients (*70*) and latitude (*17*), but as our review shows, it has not been fully appreciated and integrated in assessments of climate change effects on biodiversity.

In addition, even when climate change variables are used, instead of geographical proxies, to examine relationships with species distributional shifts, there are occasions when distributional shifts respond not only to climate but also to other environmental changes, such as spread of disease (*71*) or land-use change (*49*, *72*, *73*). Attributing a mechanism to an observed pattern thus benefits from examination of multiple alternative hypotheses on equal footing. Nevertheless, multimodal inference (*74*) was found to be extremely rare in the reviewed literature.

Last, a critical feature of science-based assessments is the ability to reproduce and build upon each other's published results. Unfortunately, many findings cannot be reproduced. Our review reveals that ~25% of the reports on distributional changes under climate change do not provide full access to the data and detailed results. Reproducibility contains several elements such as selective reporting, methods and availability of codes, statistical power, experimental design, and availability of raw data. In this review, we focused on selective reporting. However, we notice that considering other factors of reproducibility could markedly affect our assessment of published studies. Recently, a study (*75*) carried out by 1500 scientists from different disciplines (e.g., chemistry, physics, medicine, and biology) showed that most of the scientific articles are not fully reproducible; our review corroborates their findings in the subfield of climate change ecology and biogeography.

Moving forward in the capacity to assess the where, when, and why of climate change effects on biodiversity is crucial to guide the timing and magnitude of human adaptation strategies for biodiversity. In our scan of the literature, we asked very simple questions that enable establishing inferences about the quality of the underlying data and methods. We demonstrate that substantial improvements should be considered in assessments. Most of them do not require reinventing concepts or methods. Questions about the need for null models to discriminate expected directional patterns from stochastic (or more complex) ones (*65*, *76*), or the disadvantages of using indirect proxies as opposed to direct variables with proven mechanistic links to the patterns (*17*, *70*), are well established in the ecological literature. Somehow, these debates and the associated recommendations have not percolated through studies examining climate change effects on species distributions.

Our study provides a hint of the best-practice standards needed for assessments of climate change effects on a specific facet of biodiversity change: species range change. Other biodiversity change facets, such as local patterns of colonization and extinction, or abundance changes, or changes in community composition are not covered by our analysis, partly because very few of these studies exist across multiple species. Future investigations should seek to expand the facets of biodiversity change considered in quality assessments and strive to build consensus on the standards required to increase the strength of evidence of climate change impacts on biodiversity while developing detailed guidelines to help increase the robustness, transparency, and reproducibility of the assessments.

MATERIALS AND METHODS

Literature review

We identified papers by screening published reviews (*20*) and meta-analyses (*1*, *2*) and by searching the primary literature using engines such as Google Scholar, ISI Web of Science, Scopus, and Wiley Online Library. We used a combination of the following keywords in our search: "climate change" or "climate warming," "range" or "distribution," and "poleward/northward shift" or "upslope/altitudinal shift" or expansion/contraction (fig. S1). We then filtered the records by using some inclusion and exclusion criteria. These criteria comprised references that assessed distributional changes based on species occurrence data over at least two historical periods. Since our focus was on the empirically observed distributional shifts, we excluded papers that used abundance or richness data alone or those that used modeling and/or predictions to quantify "future" or "potential" changes. Our search criteria provided a set of 240 publications.

Data mining

Following the literature search, we extracted the relevant data to be structured in a suitable database (table S1). For each publication, we recorded the following information: (i) study year, (ii) spatial scale (e.g., local, regional, and continental), (iii) geographic region as reported in the study, (iv) ecosystem type (terrestrial versus marine), (v) climate zone, (vi) magnitude and direction of distributional shifts, (iv) total number of taxa and their identity (taxonomic group and species names), (vi) time period, and (vii and viii) the general methodology used by the study (table S1).

In the database, a unique code was assigned to each article reviewed and its geographic location was also recorded. To effectively visualize the spatial coverage of the reports, we digitized the geographical boundaries of all the studies reviewed as a set of either spatial polygons or points depending on the geographical extent of the study. We then used a regular 2-degree (2 × 69 miles) grid cells covering the world's land and sea areas in ArcMap software (version 10.1) to aggregate the digitized points and polygons into the grid cells and quantify the frequency of the studies at each cell.

We used the Köppen climate classification (*77*) to group the studies into the climate zones. In addition, we aggregated the spatial boundaries of the studies within the five major climatic zones defined by the Köppen climate classification based on seasonal temperature and precipitation patterns. The five climatic zones are (i) tropical, (ii) dry, (iii) temperate, (iv) continental/cold, and (v) polar.

To sort the taxonomic coverage of the data used in the studies, we first extracted the number of species and their scientific names for the given taxonomic group in each article (table S3). We added the names of species to the database, and after removing duplicate records, we calculated the proportion of species considered in studies (fig. S1).

Assessment criteria

The assessment of published studies was made following a simple set of criteria as described in Table 1. For pattern detection, we focused on the methodological aspects of the studies. We explored how the species distributional shifts were measured. Specifically, we asked whether distribution shifts were analyzed across all potential directions (e.g., latitude, longitude, and elevation), and whether the null expectation regarding distributional changes (likelihood of changes derived from patterns shifted by chance because of internal variability) was determined. Therefore, scientific publications that assessed distributional shifts within all the possible directions, rather than only along a single elevation or latitudinal axis, and also compared the results against the patterns expected by chance (null distribution) received the maximum score for the pattern detection group benchmark.

For attribution, we asked whether studies examined potential causal links between observed distributional changes and environmental predictors (e.g., climate, precipitation, and land use). We carefully reviewed the studies' methods sections to assess how (if at all) they attributed observed shifts in species distributions to climate change and what approaches were used to perform the task. The papers that investigated multiple alternative causal factors on equal footing, rather than simply examining patterns against a single predictor (e.g., temperature), received maximum score for the attribution criteria.

For reproducibility, we examined the results sections of the studies. A study received the full score for this group if the results were available for each individual species analyzed and if the divergence responses among species were fairly reported.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/15/eabe1110/DC1

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