# A globally coherent fingerprint of climate change impacts across natural systems

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**Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local, short-term biological changes. Any underlying signal from climate change is likely to be revealed by analyses that seek systematic trends across diverse species and geographic regions; however, debates within the Intergovernmental Panel on Climate Change (IPCC) reveal several definitions of a 'systematic trend'. Here, we explore these differences, apply diverse analyses to more than 1,700 species, and show that recent biological trends match climate change predictions. Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles (or metres per decade upward), and significant mean advancement of spring events by 2.3 days per decade. We define a diagnostic fingerprint of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems.**

The Intergovernmental Panel on Climate Change[1] (IPCC) assessed the extent to which recent observed changes in natural biological systems have been caused by climate change. This was a difficult task despite documented statistical correlations between changes in climate and biological changes[2–5]. With hindsight, the difficulties encountered by the IPCC can be attributed to the differences in approach between biologists and other disciplines, particularly economists. Studies in this area are, of necessity, correlational rather than experimental, and as a result, assignment of causation is inferential. This inference often comes from experimental studies of the effects of temperature and precipitation on the target species or on a related species with similar habitats. Confidence in this inferential process is subjective, and differs among disciplines, thus resulting in the first divergence of opinion within the IPCC.

The second impasse came from differences in perspective on what constitutes an 'important' factor. Anyone would consider a currently strong driver to be important, but biologists also attach importance to forces that are currently weak but are likely to persist. In contrast, economic approaches tend to discount events that will occur in the future, assigning little weight to weak but persistent forces. Differences of opinion among disciplines can therefore stem naturally from whether the principal motivation is to assess the magnitude of immediate impacts or of long-term trajectories. Most field biologists are convinced that they are already seeing important biological impacts of climate change[1–4,6–9]; however, they have encountered difficulty in convincing other academic disciplines, policy-makers and the general public. Here, we seek to improve communication, provide common ground for discussion, and give a comprehensive summary of the evidence.

How should a 'climate fingerprint' be defined? A straightforward view typical of an economist would be to conclude that climate change was important if it were principally responsible for a high proportion of current biotic changes. By this criterion a climate fingerprint appears weak. Most short-term local changes are not caused by climate change but by land-use change and by natural fluctuations in the abundance and distribution of species. This fact has been used by non-biologists to argue that climate change is of little importance to wild systems[10]. This approach, however, effectively ignores small, systematic trends that may become important in the longer term. Such underlying trends would be confounded (and often swamped) by strong forces such as habitat loss. Biologists have tended to concentrate on studies that minimize confounding factors, searching for trends in relatively undisturbed systems and then testing for significant associations with climate change. Economists have viewed this as biased (nonrandom exclusion of data) whereas biologists view this as reducing non-climatic noise. Thus, economists focus on total direct evidence and apply heavy time discounting; biologists apply a 'quality control' filter to available data, accept indirect (inferential) evidence and don't apply time discounting.

The test for a globally coherent climate fingerprint does not require that any single species show a climate change impact with 100% certitude. Rather, it seeks some defined level of confidence in a climate change signal on a global scale. Adopting the IPCC 'levels of confidence'[11] and applying the economists' view of a fingerprint, we would have "very high confidence" in a fingerprint if we estimated that more than 95% of observed changes were principally caused by climate change, "high confidence" between 95% and 67%, "medium confidence" between 33% and 67%, and "low confidence" below 33%. In contrast, the biologists' confidence level comes from the statistical probability that global biotic trends would match climate change predictions purely by chance, coupled with supporting experimental results showing causal relationships between climate and particular biological traits.

Here, we present quantitative estimates of the global biological impacts of climate change. We search for a climate fingerprint in the overall patterns, rather than critiquing each study individually. Using the biologists' approach, we synthesize a suite of correlational studies on diverse taxa over many regions to ask whether natural systems, in general, have responded to recent climate change. Furthermore, we attempt a cross-fertilization by applying an economists' measure—the estimated proportion of observed changes for which climate trends are the principal drivers—to data sets chosen using biologists' criteria. We call this a 'global coherence' approach to the detection of climate change impacts.

First, we explore a biologists' confidence assessment with two types of analyses of observed change: statistical meta-analyses of effect size in restricted data sets and more comprehensive categorical analyses of the full literature. Second, we present a probabilistic model that considers three variables: proportion of observations matching climate change predictions, numbers of competing explanations for each of those observations, and confidence in causal attribution of each observation to climate change. These three variables feature equally in a model that explores an economists' 'confidence' assessment. Finally, we explore diagnostic 'sign-switching' patterns that are predicted uniquely by climate change.

## The evidence

A few studies indicate evolutionary responses of particular species to climate change[12–14], but the generality of evolutionary response remains unknown. Here, we focus on phenological (timing) shifts, range boundary shifts, and community studies on species abundances (Table 1).

### Meta-analyses

We developed databases suitable for meta-analysis[15] on two phenomena: range-boundary changes and phenological shifts. To control for positive publishing bias, we used only multi-species studies that reported neutral and negative results as well as positive (see Methods).

For range boundaries, suitable data spanned 99 species of birds[16], butterflies[17] and alpine herbs[18,19] (see Methods). The meta-analysis showed that the range limits of species have moved on average 6.1 (±2.4) km per decade northward or m per decade upward, significantly in the direction predicted by climate change (bootstrapped 95% confidence interval of the mean ($\mathrm{CI}_{\mathrm{mean}} = 1.3$–$10.9\,\mathrm{km\,m^{-1}}$ per decade; one-sample $t$-test, degrees of freedom (d.f.) $= 98$, $t = 2.52$, $P = 0.013$; Table 2).

For phenologies, suitable data were reported for herbs[20–23], shrubs[20–25], trees[20,23–25], birds[20,21], butterflies[26] and amphibians[27,28], a total of 172 species (see Methods). There was a mean shift towards earlier spring timing of 2.3 days per decade, with a bootstrapped 95% CI of 1.7–3.2 days advancement per decade (significant at $P < 0.05$).

### Categorical analyses

The remaining studies were not included in the meta-analyses, either because they were on single species or because they did not present data in the raw form of $x$ unit change per $y$ time units per species. These less-detailed data were simplified into four categories: changed in accord with or opposite to climate change predictions, changed in some other fashion or stable (see Methods).

As with previous studies[17], analyses ignore species classified as 'stable'. This category does not represent a single result, as apparent stability could arise from a diversity of situations[17] such as: 1) the phenology, abundance or distribution of the species is not driven by climatic factors; 2) the species is actually changing, but poor data resolution could not detect small changes; and 3) the phenology, abundance or distribution of the species is driven by climatic factors, but fails to respond to current climate change. Such failure could stem from anthropogenic barriers to dispersal (habitat fragmentation) or from a lag in response time. Lags are expected when limited dispersal capabilities retard poleward/upward colonization[29], or when a necessary resource has slower response time than the focal species[17].

**Phenological shifts.** We quantitatively assessed 677 species reported in the literature (Table 1). Over a time period range of 16–132 years (median 45 yrs), 27% showed no trends in phenologies, 9% showed trends towards delayed spring events, whereas the remaining 62% showed trends towards spring advancement. Observed trends include earlier frog breeding[27,28], bird nesting[30–32], first flowering[20–25], tree budburst[23–25], and arrival of migrant birds and butterflies[20,21,26,33] (Table 1). Shifts in phenologies that have occurred are overwhelmingly (87%) in the direction expected from climate change ($P < 0.1 \times 10^{-12}$; Table 2).

**Distribution/abundance shifts.** In a quantitative assessment covering >1,046 species, we were able to categorize 893 species, functional

Table 1 **Summary of data studying phenological and distributional changes of wild species**

| Taxon | Ref. number | Total no. of species (or species groups) | Spatial scale |  |  | Time scale (range years) | Change in direction predicted ($n$) | Change opposite to prediction ($n$) | Stable ($n$) | No prediction ($n$) |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | L | R | C |  |  |  |  |  |
| Phenological changes |  |  |  |  |  |  |  |  |  |  |
| Woody plants | 20,23,24*,25* | $n = 38$ sp |  | 2 | 1 | 35–132 | 30 | 1 | 7 | – |
| Herbaceous plants | 20,21* | $n = 38$ sp | 1 | 1 |  | 63–132 | 12 | – | 26 | – |
| Mixed plants | 22* | $n = 385$ sp | 1 |  |  | 46 | 279 | 46 | 60 | – |
| Birds | 20,21*,30,31,32,33 | $n = 168$ sp | 2 | 3 | 1 | 21–132 | 78 | 14 | 76 | – |
| Insects | 26 | $n = 35$ sp |  | 1 |  | 23 | 13 | – | 22 | – |
| Amphibians | 27,28 | $n = 12$ sp | 2 |  |  | 16–99 | 9 | – | 3 | – |
| Fish | 20 | $n = 2$ sp |  | 1 |  | 132 | 2 | – | – | – |
| Distribution/abundance changes |  |  |  |  |  |  |  |  |  |  |
| Tree lines | 54,55,56* | $n = 4$ sp + 5 grps | 2 | 1 |  | 70–1,000 | 3 sp + 5 grps | – | 1 | – |
| Herbs and shrubs | 18,19,41*,42* | $n > 66$ sp, 15 detailed |  | 3 |  | 28–80 | 13 | 2 | – | – |
| Lichens | 36 | 4 biogeographic grps ($n = 329$ sp) | 1 |  |  | 22 | 43 | 9 | 113 | 164 |
| Birds | 8* | $n = 3$ sp |  | 1 |  | 50 | 3 | – | – | – |
|  | 16,57* | N sp ($n = 46$ sp) |  | 2 |  | 20–36 | 13 | 15 | 18 |  |
|  |  | S sp ($n = 73$ sp) |  | 2 |  | 20–36 | 36 | 16 | 21 | 6 |
|  | 43* | Low elevation (>91 sp) | 1 |  |  | 20 | 71 | 11 | 9 | – |
|  |  | High elevation (>96 sp) | 1 |  |  | 20 | 37 | 27 | 32 | – |
| Mammals | 37 | $n = 2$ sp |  | 1 |  | 52 | 2 | – | – | – |
| Insects | 17,49* | $n = 36$ sp |  | 1 | 1 | 98–137 | 23 | 2 | 10 | 1 |
|  | 17 | N boundaries ($n = 52$ sp) |  | 1 |  | 98 | 34 | 1 | 17 | – |
|  |  | S boundaries ($n = 40$ sp) |  | 1 |  | 98 | 10 | 2 | 28 | – |
| Reptiles and amphibians | 43* | $n = 7$ sp | 1 |  |  | 17 | 6 | – | 1 | – |
| Fish | 39 | *4* biogeographic grps ($n = 83$ sp) | 1 |  |  | – | 2 grps | – | 1 grp | 1 grp |
|  | 40* | N sp ($n > 1$ sp) |  | 1 |  | 70 | >1 | – | – | – |
|  |  | S sp ($n > 1$ sp) |  | 1 |  | 70 | >1 | – | – | – |
| Marine invertebrates | 34*,40* | N sp ($n > 21$) | 1 | 1 |  | 66–70 | >19 | 2 | – | >1 sp not classified |
|  |  | S sp ($n > 21$) | 1 | 1 |  | 66–70 | >20 | 1 | – |  |
|  |  | Cosmopolitan sp ($n = 28$ sp) | 1 |  |  | 66 | – | – | – | 28 |
| Marine zooplankton | 40* | Cold water ($n > 10$ sp) |  | 1 |  | 70 | >10 | – | – | >8 sp not classified |
|  |  | Warm water ($n > 14$ sp) |  | 1 |  | 70 | >14 | – | – |  |
|  | 35 | 6 biogeographic grps ($n \geq 36$ sp) |  |  | 1 | 39 | 6 grps | – | – | – |

N, species with generally northerly distributions (boreal/arctic); S, species with generally southerly distributions (temperate); L, local; R, regional (a substantial part of a species distribution; usually along a single range edge); C, continental (most or the whole of a species distribution). No prediction indicates that a change may have been detected, but the change was orthogonal to global warming predictions, was confounded by non-climatic factors, or there is insufficient theoretical basis for predicting how species or system would change with climate change.

*Study partially controlled for non-climatic human influences (for example, land-use change). Studies that were highly confounded with non-climatic factors were excluded. (See Supplementary Information for details of species classification.)

groups or biogeographic groups (Table 1). Less than one-third (27%) of these have exhibited stable distributions during the twentieth century. Others (24%) show changes that are impossible to relate to climate change predictions. These two types of result neither support nor refute a climate change signal, although it will be important for predictive biological models to eventually determine what proportion of these are truly stable systems.

Some range shifts have been measured directly at range boundaries, whereas others have been inferred from abundance changes within local communities. Over all of the range and abundance shift data, 434 species were categorized as changing over time periods of 17–1,000 years (median 66 years) (Table 1). Of these, 80% have shifted in accord with climate change predictions (see Methods) ($P < 0.1 \times 10^{-12}$; Table 2). New species have colonized previously 'cool' regions, including sea anemones in Monterey Bay[34] and lichens and butterflies in Europe[17,36], whereas some Arctic species have contracted in range size[35,37]. Over the past 40 years, maximum range shifts vary from 200 km (butterflies[17]) to 1,000 km (marine copepods[34]).

## Probabilistic coherence

How strong is the climate change signal in the light of confounding factors and lack of experimentation? We investigate this argument in a probabilistic context. We formulated a probabilistic model to ask whether a climate change fingerprint exists in a disparate set of $n$ observed biological changes. Let $n'/n$ indicate the proportion of observations counter to climate change predictions and $p$ indicate the probability that climate change is the only possible causal agent of the observed biological change in any of the $n - n'$ species that do conform to climate change predictions. In practice, this can be estimated across a set of species by assigning each species a 0 or a 1, depending on whether or not competing explanations exist; $p$ then is the proportion of species that have no competing explanations.

Competing (non-climatic) explanations can, therefore, be expected in $\{(1 - p)(n - n')\}$ of the reported analyses. Finally, for any of the $n - n'$ climate-conforming species, let $\pi$ indicate the probability, determined from previous empirical study, that climate change is the principal causal agent of a particular biological change (independent of $p$).

These three variables, each varying from 0 to 1, are inputs to a binomial probability model whose output estimates the proportion of all species that are, in truth, being impacted by climate change. In practice, confounding factors can never be eliminated completely from observational studies; therefore, $p$ would normally have a low value. Here, we consider only the conservative case where $p = 0$; that is, we assume that non-climatic alternative explanations exist for every species. In the Supplementary Information, we present modelling schemes where $p$ varies from 0 to 1.0.

The importance of non-climatic explanations should decrease with increasing scale. Most local changes are idiosyncratic and consist of noise when scaled up; however, atmospheric carbon dioxide levels have risen nearly uniformly across the globe. Increased $CO_2$ can directly cause earlier flowering[38], as does increased temperature, making these effects difficult to separate. However, these two effects can be viewed as different aspects of global warming, legitimizing discussion of their joint impacts.

The variable $\pi$ reflects the extent to which previous study and experimentation provides clear mechanistic understanding of the links between climate variables and a species' behaviour and ecology. To understand the importance of $\pi$, consider the case of the silver-spotted skipper butterfly (*Hesperia comma*) that has expanded its distribution close to its northern boundary in England over the past 20 years. Possible ecological explanations for this expansion are regional warming and changes in land use. Comparing the magnitudes and directions of these two factors suggests that climate change is more likely than land-use change to be the cause of expansion[29]. Deeper support was provided by previous empirical studies documenting strong thermal limitation. At the northern boundary, development of offspring was restricted to the hottest microclimates (south-facing chalk slopes). Range expansion coincided with colonization of non-southern slopes. Simulation models based solely on previously measured thermal tolerances (that is, without land-use change) closely matched the observed expansion of 16.4 km (model prediction 14.4 km)[12]. Thus, mechanistic understanding of the system generates a high estimate for $\pi$.

Figure 1 shows relationships between the $n'/n$ proportions and the minimum value of $\pi$ that would be required to sustain different degrees of confidence for $p = 0$. For example, the medium confidence region shows minimum values of $\pi$ that would be required across the displayed range of $n'/n$ proportions to guarantee that about half of the observed species impacts were in truth being driven principally by climate change. Claiming a climate fingerprint with high confidence would require high minimum values for $\pi$ ($>0.67$) regardless of $n'/n$.

## Applying the probabilistic model

Using all of the data from Table 2 to parameterize the model, $n' = 147$ and $n = 770$, making $n'/n = 0.16$ (16% of species changing opposite to climate change predictions). We now consider $\pi$. The extent to which climate change can be isolated as the predominant driving force is extremely variable among species and systems. Such attribution results from a subjective synthesis of experimental and observational research, often conducted well before and independently of any study of long-term trends. The species for which $\pi$ is high are those with a history of basic biological research, especially where research has been conducted along several axes (controlled laboratory/greenhouse experiments, field manipulations and observations).

Table 2 **Summary statistics and synthetic analyses derived from Table 1**

| Type of change | Changed as predicted | Changed opposite to prediction | *P*-value |
|---|---|---|---|
| Phenological ($N = 484/(678)$) | 87% ($n = 423$) | 13% ($n = 61$) | $<0.1 \times 10^{-12}$ |
| Distributional changes | | | |
| At poleward/upper range boundaries | 81% | 19% | – |
| At equatorial/lower range boundaries | 75% | 25% | – |
| Community (abundance) changes | | | |
| Cold-adapted species | 74% | 26% | – |
| Warm-adapted species | 91% | 9% | – |
| $N = 460/(920)$ | 81% ($n = 372$) | 19% ($n = 88$) | $<0.1 \times 10^{-12}$ |
| Meta-analyses | | | |
| Range-boundaries ($N = 99$) | 6.1 km m$^{-1}$ per decade northward/upward shift* | | 0.013 |
| Phenologies ($N = 172$) | 2.3 days per decade advancement* | | <0.05 |

Data points represent species, functional groups or biogeographic groups. *N*, number of statistically or biologically significant changes/(total number species with data reported for boundary, timing, or abundance processes). The no prediction category is not included here.

*Bootstrap 95% confidence limits for mean range boundary change are 1.26, 10.87; for mean phenological shift the limits are −1.74, −3.23.

This sort of biological detail reveals that climate and extreme weather events are mechanistically linked to body size, individual fitness and population dynamics for diverse species[3–9] (but not for all). Species for which confidence in climate as the primary driving mechanism is low are those for which long-term observational records exist, but not detailed empirical research on target species or on ecologically similar species. The black line in Fig. 1 suggests that medium confidence can be claimed for $n'/n = 0.16$ if $0.35 < \pi < 0.7$. Other contingencies, such as complications from a positive publishing bias or non-independence among confounding factors, can be considered through variations of the model (see Supplementary Information).

## Differentiating diagnostic patterns

Predictions of the impacts of climate change are not unidirectional, but may show opposite trends within communities and across long time spans or large spatial scales. Alternative causal agents would therefore have to be able to switch the sign of their impacts within a study if they were to form credible competing explanations. Such differentiating patterns greatly reduce the likelihood of hidden, non-climate competing explanations, thereby increasing $P$ and decreasing the value of $\pi$ necessary to achieve a given confidence level (see Supplementary Information). High confidence could be obtained under this scheme with existing patterns ($n'/n \leq 0.33$) and poor mechanistic understanding (low $\pi$). Sufficient data to quantify the differential impacts on species' distributions or phenologies across time periods or geographic regions were available for 334 species, among which 84% showed a sign-switching diagnostic of climate change response ($P < 0.1 \times 10^{-12}$; Table 3).

### Community representation sign switching

Community studies in regions of overlapping 'polar' and 'temperate' species base their climate change attribution on differential responses of these two categories. Among marine fish and intertidal invertebrates (for example, snails, barnacles, anemones, copepods and limpets) off the Californian coast[34,39] and in the North Atlantic[35,40], lichens in the Netherlands[36], foxes in Canada[37] and birds in Great Britain[16], polar species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions. Analogous shifts are occurring even within the Arctic and Antarctic among penguins[8], woody plants[41] and vascular plants[42]. Similar patterns exist for lowland compared with highland birds in the tropics[43]. Most of these studies are local, with high variability of individual species' population dynamics. Even so, 80% of changes in community representation are in accord with climate change predictions (Tables 2 and 3).

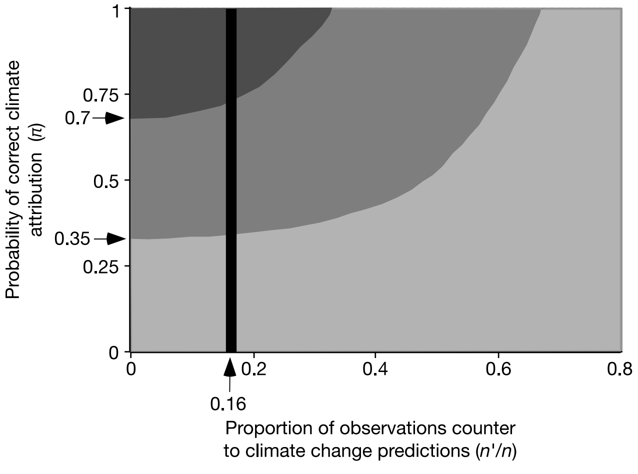

**Figure 1** Probabilistic model based on parameter estimates from a review of the literature. Levels of confidence in the linkage of biological changes to global climate change are: high (dark grey), medium (mid-grey) and low (light grey). Confidence regions assume $p = 0$ (competing explanations exist for all studies). The black line indicates the region of confidence possible using the probabilistic model on the basis of the parameter estimate of $n'/n$ from the literature review, and allowing $\pi$ to vary freely.

### Temporal sign switching

Long-term studies encompass periods of climate cooling as well as warming. If the distributions of species are truly driven by climate trends, these species should show opposite responses to cooling and warming periods. Such sign switching has been documented in the United Kingdom for marine fish, limpets, barnacles and zooplankton[40], in the United Kingdom and Estonia for birds[20,31,44,45], and in the United Kingdom, Finland and Sweden for butterflies[17,46–48] (see also Table 3 legend). A typical pattern includes northward range shifts during the two twentieth-century warming periods (1930–45 and 1975–99), and southward shifts during the intervening cooling period (1950–70). No species showed opposing temporal trends (Table 3).

### Spatial sign switching

Whole-range, continental-scale studies, by encompassing the extremes of a species' distribution, allow testing for differential spatial impacts. In North America and Europe, detailed temporal data spanning the twentieth century were compiled for 36 butterfly species at both northern and southern range extremes[17,49]. Eight species (22%) exhibited a diagnostic pattern of northward expansion (new colonizations) and southern contraction (population extinctions). No species showed opposing range shift trends (northward contraction and southward expansion) (Table 3).

## Discussion

The logic of a global focus on biological change is analogous to that for climate change itself. With climate change, attribution of recent warming trends to changes in atmospheric gases comes from analysis of global patterns, not from detailed data from individual meteorological stations. Similarly, when assessing biological

Table 3 **Biological fingerprint of climate change impacts**

| Sign-switching pattern | Percentage of species showing diagnostic pattern |
|---|---|
| Community | |
| Abundance changes have gone in opposite directions for cold-adapted compared with warm-adapted species. Usually local, but many species in each category. Diverse taxa, $n = 282$*. | 80% |
| Temporal | |
| Advancement of timing of northward expansion in warm decades (1930s/40s and 1980s/90s); delay of timing or southward contraction in cool decades (1950s/60s), 30–132 years per species. Diverse taxa, $n = 44$*. | 100% |
| Spatial | |
| Species exhibit different responses at extremes of range boundary during a particular climate phase. Data are from substantial parts of both northern and southern range boundaries for each species. All species are northern hemisphere butterflies, $n = 8$*. | 100% |

Differential sign-switching patterns diagnostic of climate change as the underlying driver.
*Numbers of species represent minimum estimates, as not all species were described in sufficient detail in each study to classify. A few species showed two types of sign switching, and so are included in more than one cell. Data are from references in text and from raw data provided by L. Kaila, J. Kullberg, J. J. Lennon, N. Ryrholm, C. D. Thomas, J. A. Thomas and M. Warren.

impacts, the global pattern of change is far more important than any individual study.

The approach of biologists selects study systems to minimize confounding factors and deduces a strong climate signal both from systematic trends across studies and from empirically derived links between climate and biological systems. This deduction is made even if climate explains only a small part of the observed biological change. The meta-analyses of 334 species and the global analyses of 1,570 species (or functional/biogeographic groups) show highly significant, nonrandom patterns of change in accord with observed climate warming in the twentieth century, indicating a very high confidence (>95%) in a global climate change fingerprint (Table 2).

The approach of economists takes a broader view. In its purest form, applied to all existing data and incorporating time discounting, this approach would conclude that climate change has little total impact on wild species. We argue that this approach misses biologically important phenomena. Here we hybridize the two approaches by applying an economists' model to data that biologists would consider reasonable, and forego time discounting. A total of 74–91% of species that have changed have done so in accord with climate change predictions (Table 2) giving an estimate of $n'/n = 0.16$ for the hybrid model. Assessment of $\pi$, the probability of correct attribution to climate, is subjective and relies on the level of confidence in inferential evidence. Such evidence comes from empirical analyses and experimental manipulations, which have documented the importance of climatic variables to the dynamics, distributions and behaviour of species[3,5,8,9]. From these studies, biologists infer that expected values of $\pi$ are often high. We show that moderate values of $\pi$ (0.35–0.70) are consistent with medium confidence in a global climate change fingerprint.

The different approaches raise two distinct questions of the data and result in different levels of confidence in a climate change fingerprint. The questions are: (1) whether climate change can be shown to be an over-riding factor currently driving natural systems; and (2) whether there is sufficient evidence to implicate climate change as a common force impacting natural systems on a global scale. In an absolute sense, land-use change has probably been a stronger driver of twentieth century changes in wild plants and animals than has climate change (question 1). From a biological view, however, finding any significant climate signal amidst noisy biological data is unexpected in the absence of real climate drivers (question 2). Such small, persistent forces are inherently important in that they can alter species interactions, de-stabilize communities and drive major biome shifts.

A review of the literature reveals that the patterns that are being documented in natural systems are surprisingly simple, despite the real and potential complexity of biotic change. Change in any individual species, taxon or geographic region may have a number of possible explanations, but the overall effects of most confounding factors decline with increasing numbers of species/systems studied. Similarly, uncertainty in climate attribution for any particular study does not prevent the development of a global conclusion on the basis of a cumulative synthesis. In particular, a clear pattern emerges of temporal and spatial sign switches in biotic trends uniquely predicted as responses to climate change. With 279 species (84%) showing predicted sign switches, this diagnostic indicator increases confidence in a climate change fingerprint from either viewpoint.

The published IPCC conclusion stated high confidence ($P > 0.67$) in a climate signal across observed biotic and abiotic changes. Analyses presented here support that conclusion. Furthermore, a driver of small magnitude but consistent impact is important in that it systematically affects century-scale biological trajectories and ultimately the persistence of species. The climate fingerprint found here implicates climate change as an important driving force on natural systems. ☐

## Methods

### Climate change predictions

Expected phenological shifts for regions experiencing warming trends are for earlier spring events (for example, migrant arrival times, peak flight date, budburst, nesting, egg-laying, and flowering) and for later autumn events (for example, leaf fall, migrant departure times, and hibernation)[50,51]. Response to climate warming predicts a preponderance of polward/upward shifts[50,51]. Dynamics at the range boundaries are expected to be more influenced by climate than are dynamics within the interior of a species range. Thus, community level studies of abundance changes are used best to infer range shifts when they are located at ecotones involving species having fundamentally different geographic ranges: higher compared with lower latitudes, or upper compared with lower altitudes. Response to climate warming predicts that southerly species should outperform northerly species at the same site[50,51].

### Selection of studies for review

This was not an exhaustive review. The studies listed in Table 1 comprise the bulk of wild species studied with respect to climate change hypotheses. Selection of papers was aimed at those with one or more of the following attributes: long temporal span (>20 years), data covering a large geographic region, and/or data gathered in an unbiased manner for a multi-species assemblage (typically species abundance data of locally well-documented communities). We excluded several high-quality studies of single species performed at local scale or highly confounded by non-climatic global change factors. The stable category represents species for which any observed changes are indistinguishable from year to year fluctuations, either from a statistical test for trend using very long time series data or from comparing net long-term movement to expected yearly variation on the basis of basic biological knowledge of dispersal/colonization abilities.

### Meta-analyses

To create databases, studies were combined that made similar types of measurements and that reported quantitative estimates of change over a specified time period. All species were used; that is, even species that are categorized as stable in Table 1 were included in the meta-analysis. We treated phenological and distributional changes separately. To minimize positive publishing bias, only multi-species studies were included.

We considered each species as an independent data point, rather than each study. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species.

We used only distributional studies at range boundaries. We excluded equatorial and lower elevational boundaries because of a paucity of data combined with theoretical reasons for treating these boundaries separately from poleward/upper elevational boundaries[52]. Three studies met the criteria for data detail, covering 9 alpine herbs[18,19], 59 birds[16] and 31 butterflies[17]. The geographic locations of these boundaries were non-overlapping, reducing the likelihood of correlated confounding variables. Altitude was converted to latitudinal equivalent (for temperature clines, 1 km northward = 1 m upward). The United Kingdom bird data compared mean northern boundary in 1999 to that in 1972 using the ten northernmost occupied grid cells (on 10 km$^2$ grids) from published atlases. The Swedish butterfly data compared mean northern boundary in the period 1971–97 to mean northern boundary in 1900–20 using the five northernmost records per year. The Swiss herb data showed changes in species assemblages over the twentieth century in fixed plots up altitudinal gradients on 26 mountains.

The effect size per species was the absolute magnitude of range boundary shift, standardized across species to be in units of km m$^{-1}$ per decade, with northward/upslope shifts positive and southward/downslope shifts negative. Data were not skewed, and $n$ was large. Therefore, a one-sample $t$-test was used to evaluate the null hypothesis of no overall trends (that is, $H_o$: mean boundary change across all species is zero). Variances were not available for all species, so we used an unweighted analysis. We performed an additional bootstrap analysis of 95% confidence limits on the mean boundary shift (10,000 iterations)[53].

The phenological meta-analysis was on spring timing events—there were insufficient studies on autumn phenology to warrant analysis. Nine studies published magnitudes of shift over a given time period (17–61 years). They included 11 trees[20,23–25], 6 shrubs[20,21,23–25], 85 herbs[20–23], 35 butterflies[26], 21 birds[21], 12 amphibians[27,28] and 2 fish[20]. This data set was inappropriate for the $t$-test owing to skew, but bootstrapped confidence limits provided an estimate of the probability that the true mean shift includes zero.

For both analyses, geography and taxa are confounded. For the range boundary analysis, all bird data are from the United Kingdom, all butterfly data from Sweden, and all herb data from Switzerland. For the phenological analysis, most shrub and bird data are from the United States, butterfly data from Great Britain, and trees from Europe. Therefore, it is not meaningful to split the analyses further.

### Categorical analyses

Reported data from all studies listed in Tables 1 and 3 were included in the categorical analyses. The predicted direction is a change predicted by global warming scenarios[50,51]. All studies were conducted in temperate Northern Hemisphere, except for 194 species in Costa Rica[43] and 5 species in Antarctica[8,42]. Two categories showing changes either predicted by or opposite to predictions of climate change theory were tested against the random expectation of an equal probability of observing changes in either direction. Analyses were by binomial test with $H_o$: $P = 0.5$.

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