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Climate Disruption and Biodiversity

Review

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'Global warming' may be a familiar term, but it is seriously misleading. Human actions are causing a massive disruption to the planet's climate that is severe, rapid, very variable over space and time, and highly complex. The biosphere itself is complex and its responses to even simple changes are difficult to predict in detail. One can likely only be certain that many changes will be unexpected and some unfortunate. Even the simple, slow warming of the climate will produce complex consequences to species numbers and distributions because of how species depend on each other. An alternative approach to worrying about details is to concentrate on understanding the most significant ecological changes, ones that are irreversible — so-called 'tipping points'. Once such a point has been passed, even if society managed to restore historical climatic conditions, it might not restore the historical ecological patterns. Nowhere is this more obvious than in the loss of species, for we cannot recreate them. Climate disruptions may cause the loss of a large fraction of the planet's biodiversity, even if the only mechanism were to be species ranges moving uphill as temperatures rise.

Introduction

'Global warming' is now a phrase of on everyone's lips — it has more than 50 million hits on Google. Its combination with biodiversity — the variety of life on Earth — gets more than a million hits, barely 15 years since Peters and Lovejoy [1] convened the first meeting on the subject. The phrase is appealing, but seriously misleading [2]. Earth is experiencing a rapid global disruption to its climate, one of considerable physical complexity [3,4]. Even if we were to consider just individual species and assumed each responded independently — and only to a warming climate — then the ecological consequences would be complex enough. The interactions between species in the intricate networks we call food webs are themselves elaborate and add further complexities. There is likely no hope of ever predicting the detailed consequences of climate disruption to a particular species any more than we can predict the outcome of tossed dice. Our inability to predict in detail whether (say) dengue fever [5] or other typically tropical diseases [6] or agricultural pests [7,8] will spread beyond their existing ranges, and if so how quickly and how far, is potentially catastrophic.

Perhaps because of these difficulties, there is much discussion of *tipping points*. This term gets 500,000 hits on Google, though I find that it is generally poorly defined and its use is often simple attention-grabbing and rarely well-justified. Does it mean that it is irreversible or that small changes sometimes have large and long-term consequences (or both)? The latter is easy to imagine and I think is what most mean by the term. The former requires special circumstances that lead to reversals being genuinely impossible. If we are effecting truly irreversible changes, then climate disruption is very serious indeed.

A commonly cited 'tipping point' is the melting sea ice of the Arctic Ocean. Once gone, or seriously reduced, a variety of factors may tend to keep the ocean ice-free for centuries. That is not quite the same as never coming back. Yet, it might have consequences that are incontrovertibly irreversible. If, because of melting ice, polar bears [9] or ivory gulls [10] become extinct, we cannot reverse their loss. We do not live in Jurassic Park — even if Senator James Imhoff requested testimony on global change from the author of that fictional work to a United States of America Senate committee hearing on global change that Imhoff chaired in September 2005.

Of course, all modern species are survivors of cycles of freezing and thawing that have occurred since the Pleistocene. But if species extinctions increase dramatically with our present climate disruption, exacerbated with other human impacts, then Earth cannot ever be the same as it was before that disruption. Extinction really is forever. My central question is: how does climate disruption cause the loss of biodiversity?

The Complexity of Climate Change

Figure 1 shows that the patterns of climate change in the last century and predicted future disruptions are not just of temperature; that they are not uniform across the planet; and that neither they nor their consequences are gradual. Hansen *et al.* [11] show that the global average temperature has increased by about 0.2°C per decade, when comparing the years since 2000 to the period 1951 to 1980. Warming manifests itself not just in increasing temperatures (Figure 1, top left), however, but in other phenomena that likely have direct ecological consequences, such as the declining extent of the winter snow cover in the northern hemisphere (Figure 1, top right) [4] and fewer days when northern latitude rivers are icebound (Figure 1, middle left) [12].

Focussing just on average temperatures sweeps under the carpet the extremes of hot and cold, their geographic distribution, and their timing. Areas north of 65°N have warmed substantially more than areas between 20°N and 20°S (Figure 1, top left) [3]. Even within Canada, data from the United States National Center for Snow and Ice show that the decline in days when rivers are icebound is far greater in the far north (Coppermine River, at 68°N, Figure 1, middle left) than further south (Red River, at 50°N, Figure 1, middle left).

Likewise, associated global averages of rainfall are incomplete — some places have become wetter and others drier in the last century [3]. Following locality suggestions from [3], Figure 1 (bottom) shows data from the National Oceanic and Atmospheric Administration's National Climatic Data Center for Niger and Argentina that typify regional patterns. Niger straddles one of the more extreme ecological gradients on Earth. Sites in its more mesic south receive nearly a hundred times more rain than those in its desert north. The latter show a consistent drying trend over the last century, while the former do not (Figure 1, bottom left) [3].

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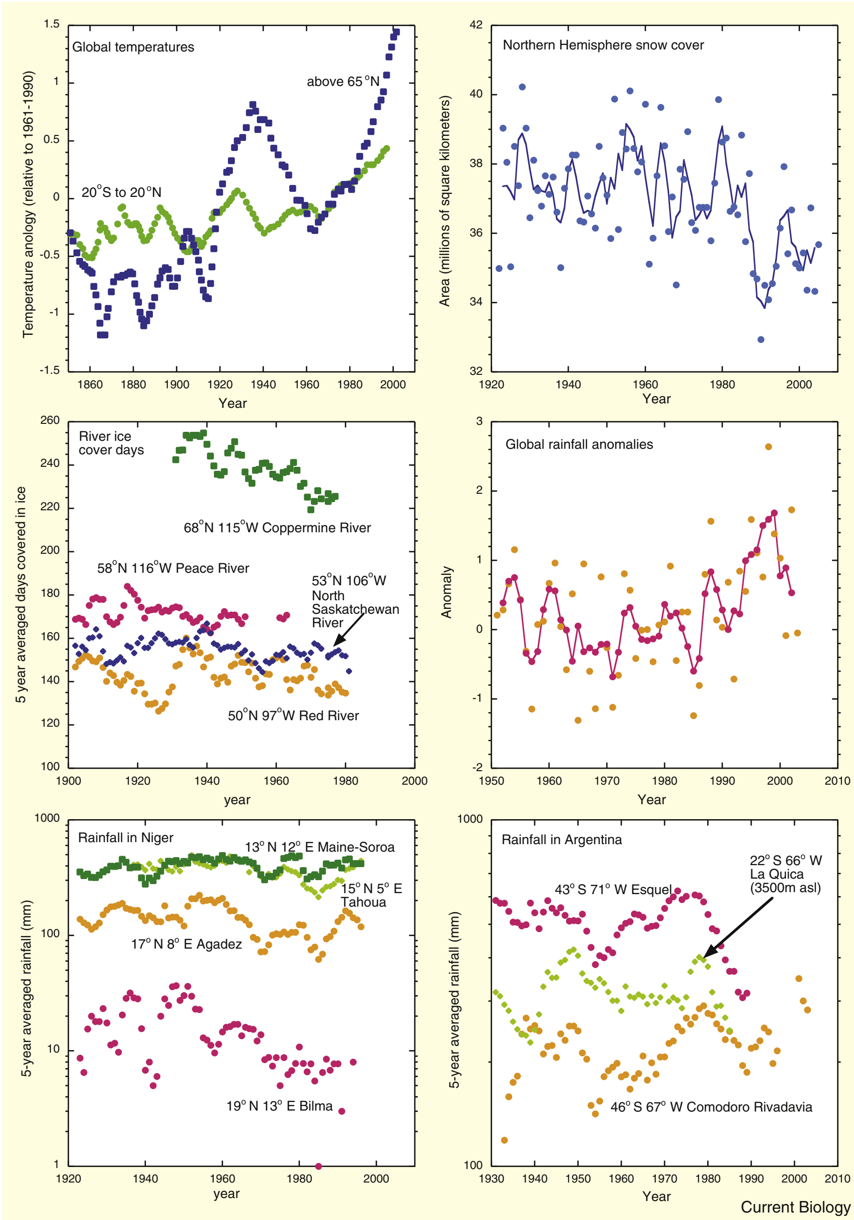

Figure 1. The complexity of climate disruption.

The physical consequences of climate disruption are more complex than a simple uniform, globally homogenous increase in temperature as these examples illustrate. Top left: moving averages of temperature averaged over site above 65°N and between 20°N and 20°S (after [3]). Top right: area of snow cover in the Northern Hemisphere, with three year moving average (after [4]). Middle left: days of ice cover of selected Canadian rivers, downloaded from http://nsidc.org/data/G01377.html. Middle right: global rainfall anomalies and their 3-year moving averages (after [3]). Bottom: 5-year moving averages of selected long-term data on rainfall, downloaded from http://www1.ncdc.noaa.gov, but selected to be regionally representative from [3].

In contrast, dry, coastal areas in Argentina and adjacent countries have shown a long-term trend towards *more* rainfall, while sites closer to the Andes have not [3].

Not surprisingly, models of future changes also show complex regional changes and the various models disagree on how large and exactly where the different changes will take place. These models predict even average temperature changes at a spatial scale orders of magnitude larger than even quite coarse ecological divisions [13]. Those divisions are themselves likely too large to allow ecologists to make specific predictions about how climate changes will affect ecological communities.

Average temperature changes do not in themselves provide simple predictions about ecological consequences. Average temperatures have changed more in high latitudes than in the tropics (Figure 1, top left), but tropical species are likely more sensitive to temperature changes than temperate ones [14].

Worse still is that it is often not the averages that matter but extreme events. Averages miss details of snowfall and melting snow and of local rainfall, whether gentle or torrential. There are changes in whether winds blow steadily or come episodically as hurricanes, and on down a long list of changes any one of which can have profound effects on the biosphere. These details matter ecologically: Adelie penguins (Figure 2) decline because of increasing snowfall in Antarctica [15] and turtle nests fail in the Caribbean when hurricanes wash them out [16]. There are limited data on climatic extremes, but there seems to be an increase in the amount of rain that comes during exceptionally wet days (Figure 1, middle right).

Hansen *et al.*'s map suggests that almost all of Europe has warmed by about 1°C [11]. One's intuition might suggest that the species least likely to suffer from climate changes is our own. We can bundle up when it is cold, drink more water when it is hot or simply move indoors when the weather outside is inclement. Yet, an excess of 70,000 people died across Europe during the hot summer of 2003 [17]. As is typical of other species, the elderly and the sick were the most vulnerable [17]. Averages hide extremes, and extreme, local events can be what drive the important ecological (and social) changes.

The very complexity of the physical changes means that we are unlikely to predict the ecological changes in any detail. It gets worse. Ecosystems themselves are so complex that we cannot predict the specific details of a species' abundance and geographical range when other species change.

Small Inputs, Large Consequences

Politically motivated critics of global warming often note how small is the concentration of CO_2 in the atmosphere or how small is the expected change in average temperature compared to the range experienced from day-to-day — as

Figure 2. Species suffer in complex ways from climate disruption.

(A) Models predicted that the red-backed shrike would greatly increase its range from 1970 to 1990 within the British Isles. In fact, it stopped breeding there. (B) The grey-winged cotinga lives in cloud forest in coastal Brazil which will likely be gone if the annual temperature increases more than a degree or so. (C) Increased snowfall reduces the nesting success of the Adelie penquin. (D) In some areas, pied flycatchers arrive too late to feed caterpillars to their nestlings. (E) The silver-spotted skipper has increased its range faster than expected because it now can reach habitats too distant in the past to colonize. (F) Edith's checkerspot butterfly has disappeared from some of the montane areas where it previously lived in the past. Photos courtesy of: (A) R. van Aarde; (B,C) the author; (D) C. Both; (E) Z. Davies; (F) P.R. Ehrlich.

if such arguments provided some proof of their inconsequence [18]. There are abundant examples in nature where small changes accompany surprisingly large effects.

Perhaps the simplest example is the subject of so many school or college ecology field trips: a visit to a hillside. The difference in elevation of a few hundred metres — a change corresponding to perhaps 1°C in average annual temperature — can change the forest from a deciduous to a coniferous one or a coniferous forest into tundra. In other words, the boundaries between very different ecosystems depend on very small differences in temperature.

The alternative to comparing different places at one instant is to examine the same place over time as the climate has warmed. Root *et al.* [19] compiled data on when bird migrants arrived in the spring, birds laid their eggs, and when plants flowered. These are often based on popular observations of amateur naturalists, some of whom keep records that span their lifetimes — especially in Britain and western Europe where winters are long and wretched and the first signs of Spring are correspondingly welcome. Of 1468 sets of records, 1190 (81%) showed events happening earlier in the seasons, on average 5 days per decade. Similarly, Fitter [20] examined 385 species of British plants and found that they flowered an average of 4.5 days earlier from 1991 to 2000 compared to the 1954 to 1990 mean. Parmesan [21] provides an extensive review of comparable studies.

Entire ecosystems change too. An obvious example involves the role of fire. Seemingly small changes in annual temperature and rainfall can greatly increase fire frequencies. Westerling *et al.* [22] show that wildfires have increased four-fold in 30 years in the western USA, while historical events, such as the 'Little Ice Age' around 1600, dramatically decreased fire frequencies in other parts of the USA [23].

Such examples open the possibility that any of a long list of climate disruptions may produce changes to biodiversity that are highly significant to us.

Complexity Catastrophes

As the climate warms, species will surely not march in orderly rows towards the warming poles or up mountainsides. As glaciers retreated over the past ten millennia, mammal species moved at very different rates northwards through North America and Europe [24]. That means that historically there were communities composed of species that seem very improbable neighbours to us now. In North America, three species characteristic of today's boreal forest — yellow-cheeked vole, northern bog lemming, and arctic shrew — were once part of mammal communities in deciduous forests and grasslands [24]. Future predictions of the California flora suggest it will be torn apart as some species will move northwards while others, presently living nearby, will move upslope, roughly eastwards into higher elevations in the Sierra Nevada [25].

Darwin famously ends *Origin of Species* with a metaphor of an "entangled bank… with (species) dependent on each other in so complex a manner" [26]. Extending that metaphor: in the post-Pleistocene warming, the existing tangled banks were taken apart as species moved at different rates and hitherto un-encountered banks reassembled. The present rate of warming is much faster, so orderly changes will be even less likely.

Surely, we might expect some simple patterns! A herbivore should move pole-ward or upslope more slowly than its plant food, because the latter must be there first to support it. In general, moving species might leave their enemies behind — at least until they catch up. Leaving enemies behind should give species an advantage. Nature cruelly dashes such naïve speculations. A wealth of empirical studies show that almost half the species in experimental species-removal studies become *less* abundant when their enemies are absent [27]. Theoretical studies confirm the likelihood of such counter-intuitive outcomes and provide the explanation [28]. A herbivore may benefit from the loss of its predator, but suffer more harm from a competitor that the predator had kept at low numbers.

Thomas *et al.* [29] describe several synergistic mechanisms — changes in the ability of insects to move through habitat patches, changes in their food supply, and in their ability to disperse — that lead to geographical ranges expanding *faster* than expected. The mechanisms they document are idiosyncratic and capricious.

The silver-spotted skipper once lived only on warm, south-facing chalk hillsides in southeast England (Figure 2). Now it lives even on north-facing slopes there. Like other butterflies, the skipper has many subpopulations that are more or less isolated from each other, reflecting the patchy distribution of suitable breeding habitats. Some patches of habitat were too small or too isolated to support persistent butterfly populations. Thomas *et al.* [29] argue that a warming climate created more and larger patches. These patches provided steppingstones to yet other suitable patches that were previously too remote or too small to have been occupied permanently. With climate warming, the total area of habitat available to the silver-spotted skipper has doubled since 1982, but the butterfly's geographical range has expanded threefold.

Thomas *et al.* [29] also studied the distribution of the brown argus butterfly in Britain. It expanded from the 1970s to the 1990s. In the south of England, the range has filled in previously unoccupied areas. In the north, the range expanded considerably from what was previously only sporadic occurrence. As Thomas *et al.* [29] reveal, there was a change in the butterfly's choice of host plant, from sun-loving *Helianthemum chamaecistus* to *Geranium* species. The latter live in habitats that were previously too cold for this butterfly. Indeed, the authors find that the larvae grow faster on the widely distributed geraniums. Spreading into patches of geraniums has allowed the butterfly to cross the previously impossibly large gaps in the distribution of *Helianthemum*.

An even more complex example involves the pied flycatcher, a small insectivorous bird that migrates to Western Europe from Africa each spring, returning in the autumn (Figure 2). The bird readily nests in artificial nest boxes, making it a popular study subject [30]. Caterpillars are a key resource for the nestlings and their numbers peak in the spring. The caterpillar peaks differ from place-to-place, from the first week of May in some places until the end of May in others, and the peaks now occur much earlier than in the past. Although the birds arrive earlier than they did in the past, they arrive too late in places with the earliest caterpillar peaks. In such places, the local numbers of the birds have declined to 10% of their former numbers [31].

These examples are not comprehensive. They are enough to show that species responses to warming are extraordinarily complex. They are sufficient to show that while we might, after-the-fact, understand why some species move faster than others, some do better and some do worse, predicting any specific outcome is likely impossible.

Tipping Points

An entirely different level of impact comes from considering tipping points. A change may be complex and unexpectedly fast, but not necessarily irreversible. Ecosystem ecology has a long tradition of thinking about alternative ecosystem states, where human actions or natural changes flip an ecosystem from one state to another, and with little chance of the reverse flip. Empirical evidence is altogether harder to obtain, largely because showing that an ecosystem has remained in a different state for a long time requires a long time series. A plausible mechanism for why the system has not reverted to its original state is also helpful.

Recently, Lenton *et al.* [32], who are careful to define tipping points, listed 15 possible examples involving large-scale changes. Almost all involve purely physical feedbacks, of which the melting arctic sea-ice is one of the fastest. And with familiar mechanisms too: when a surface is covered with snow or ice, much sunlight is reflected, but once the cover begins to break, the ground itself absorbs more energy, warms, then melts more snow and ice. Earth has likely experienced such changes before. Whatever the mechanisms, severe and very long-term consequences to the biosphere will follow.

Some tipping points, however, involve complex interactions between the biosphere, human actions, and climate. These changes are surely novel ones in Earth's history.

Dryland ecosystems — those lacking trees — cover about half the Earth's ice-free land surface [33]. They have already been massively degraded by human actions (and especially our livestock) [33]. A compelling example of a human–climate interaction is documented in *The Changing Mile,* a remarkable book by Hastings and Turner [34] that compared new and century-old photographs of southern Arizona. By 1854, contemporary accounts are of streams running through open land with plentiful grass. Settlers came in under the protection of the US Army and the railroad arrived in 1880. The Arizona Territory held 5,000 head of cattle in 1870 and 1.5 million by 1891. In 1891 and 1892 the summer rains failed. By early 1893, perhaps three-quarters of the herds died.

Along the U.S. border, the surveyors in 1891 recorded that, apart from the sparser grass, places were unchanged from their descriptions three decades previously. "The descent is made by a succession of terraces. Though affording no great quantity of water, the river is backed up into a series of large pools by beaver dams and full of fish." In the 1960 photograph, the grasses are gone and the watercourse is deeply scoured with steep sides. "Arroyo cutting" started in the drought of the 1880s. The loss of vegetation opened up the soil to erosion. Water cut deep channels into what was once gently sloping prairies. As if this were not bad enough, the deeper channels allowed more water to run off the land, so less water remained in the soil to support already stressed grasses.

These are not changes attributable to recent climate disruption, of course. Indeed, what makes them interesting is that they occurred long enough ago that the failure to recover suggests that there really is some point beyond which changes are not quickly reversible. Yet, the collision of changes in climate and human presence are seriously worrying for this and similar ecosystems globally.

Climate disruption is likely to exacerbate the damage and, through the mechanisms involved in the Arizona example, change grasslands into deserts for the long-term. Across much of Africa, Australia and southwest Asia, the century long trend is for increasing drought ([4], p. 257), and the incidence of unusually wet days and consequent flooding has increased in many places ([4], p. 303). And human population numbers — and those of their necessary livestock — are growing exponentially, putting yet greater pressure on already stressed dryland ecosystems. To complicate things further, Bond [35] suggests that widespread increases of woody plants in savannahs may be partly due to the increased atmospheric CO_2.

Tropical moist forests are forests warm enough to not experience frosts and wet enough year-round to not experience seasonal loss of leaves. They once covered 15% of the terrestrial land surface [33]. Deforestation is reducing their area rapidly. The largest remaining block is the Amazon, where deforestation and human-caused fires go hand in hand. The incidence of fire depends on at least three main factors [36]. The incidence declines exponentially with distance to roads. Given that distance, there are far fewer fires in protected areas (including national parks and indigenous reserves). Importantly, given both these factors, the majority of fires occur in the few drought years that accompany El Niño events.

Human actions alone can generate a cycle whereby a fire thins out a forest, making it drier and more open and so susceptible to another fire, until open areas or dry forest replace the original moist forest. What makes the Amazon a candidate for a tipping point is that the Amazon generates much of its own rainfall in a cycle of rain, evaporation, and more rain as the air flows across its surface [37]. Models of future Amazon deforestation typically generate 20–30% reductions in rainfall and an increase in the length of the dry season. El Niño caused droughts will be more severe, bringing more fires and more drying [38].

Species Extinction Is Irreversible

Human actions to date have already raised species extinction rates to one hundred times their natural, background rates and are poised to inflate that rate to one thousand times background in the next few decades [33]. Those human actions include habitat destruction, the introductions of species to parts of the world where they do not belong and over-hunting and over-harvesting. Two obvious questions about climate disruption are: will it cause the demise of large numbers of species and, because a species cannot go extinct twice, are the species that global change dooms different from the ones that habitat losses have exterminated or soon will [39]?

Climate disruption may eliminate species through any of the complex (and so unpredictable) interactions with other species discussed above. There is, however, one simple and easy-to-imagine mechanism: range shrinking. As the climate warms, we might expect that ranges will move to keep species within their familiar envelope of climatic experience. For some species — those on mountain tops, for example, that envelope may shrink to nothing and the species will become extinct (Figure 2).

From a theoretical viewpoint, this is a hugely seductive exercise, because anyone with modest programming skills can readily find data on present species distributions, fit them with statistical methods to present climate variables, and then determine future distributions. The models produce voluminous output of where species will be in the future under many different climate warming scenarios and model assumptions. This is a growth industry [25,40–44] and it begs the obvious question: do models of climate changes over the last decades do a reasonable job of predicting the observed changes in species ranges?

Araujo and Rahbek [45] argue that the answer is "no." For example, the observed and predicted distributions of 90% of 116 British birds "differed markedly". They fit models to species distributions in the 1970s, predicted the ranges expected in the 1990s and compared them to those observed. Given the complexities described above, perhaps one should not expect a good match. Indeed, even the models themselves involve many climate scenarios and the combinations of many assumptions. Such efforts always beg the questions of "why did they do it that way, and if I had done it differently would it have made an important difference?"

What these models do, however, is hint at the size and location of the extinctions warming may cause. Sekercioglu *et al.*[44] predict that 400 to 550 of the world's 8500 landbird species will go extinct by 2100 with a warming estimate of 2.8°C. A further 2150 species will be at risk of extinction. Perhaps their most alarming prediction is that only about one-fifth of these species are presently on the watch-list of species at risk of extinction [46]. That list already contains about 12% of the world's birds, ones mostly threatened by habitat loss. Jetz *et al.* [40] and Thomas *et al* [29] have broadly similar estimates.

Most importantly, increasing numbers of empirical studies show local extinction of isolated montane populations as the climate warms. A good case history is Edith's checkerspot butterfly (Figure 2), a species with a large but fragmented range running from Mexico to Canada. A resurvey in 1993 to 1996 of populations known in the previous century showed that more than 40% of the populations below 2400 m above sea-level had gone extinct, whereas only 15% of the populations from 2400 to 3500 m had done so [47].

Less direct studies follow increases in elevation over previous decades, a method that obviously depends on there being earlier surveys. Moritz *et al.* [48] examined 28 mammal species in Yosemite National Park, resurveying an elevational gradient first studied a century ago. The elevation limits of half the species moved an average of 500 meters upwards, consistent with the observed 3°C increase in minimum temperatures. A comparable study of moths in Mount Kinabalu (Borneo) found increases of 67 meters in elevation over 42 years [49] with two-thirds of the 102 species moving upslope, while the remainder did not. Likewise, Lenoir *et al.* [50] found that 171 European plant species moved up an average of 29 meters per decade, again with about two-thirds of the species moving upslope.

Stripped of their complexities, what drives the modelled estimates of species extinctions are basic empirical observations. First, the species the most vulnerable to extinction are those with the smallest geographical ranges and they are concentrated in the tropics [51]. Second, the only way is up. If a mountain is nearby, the way to cool off is to climb it: temperature gradients on tropical mountains can be steep — 5.2 to 6.5°C per 1000 m. In contrast, one would travel 1000 *kilometers* in temperate regions to cool an average of 6.9°C. Tropical gradients are much lower. (A warm wet forest at, say, La Selva Costa Rica is not noticeably cooler, with an annual average temperature of 25.8°C, than one at Manaus 1000 km to the south on the Amazon with an annual average temperature of 26.6°C [52].) Third, many species live on mountains. Of New World landbirds, for example, over 20% of species live above 1000 m above sea level [51].

Thus, independent of model assumptions, we know that a substantial fraction of some groups of species live in montane areas and close enough to the peaks that their present climate preferences will disappear with the simple expected increases in annual temperature. We also know empirically that roughly a half to two-thirds of species studied will move upslope if they need to maintain their present climate preferences. These observations alone suggest the minimum impacts of climate disruption will cause significant losses of species.

What We Do Not Know

Since 1994 [1], the progress in understanding the effects of climate disruption on biodiversity has been spectacular. Climate scientists are providing ever better documentation of changes in the last decades and predictions of future changes. Nonetheless, this is an expanding field. Ecologists are only just beginning to assimilate the consequences of simple increases in temperature and some gaps in knowledge are obvious.

First, the ecological consequences of the myriad of other possible climate effects — especially extreme ones that are by definition both statistically rare and potentially powerful — are still poorly known.

Second, the ecological response to even simple changes can be bewilderingly complex. Surely, all generalizations will be false. Understanding how individual species will change will require detailed, specific case studies.

Third, there is considerable potential for large-scale long-term changes, some of which might indeed be reversible and thus involve 'tipping points'. I considered three case histories — the Arctic, drylands, and rainforests — but these do not exhaust the catalogue of possible tipping points. They are enough to suggest that climate disruption to environments already heavily impacted by human actions can lead to at least very long-term changes — and do so across a wide variety of ecosystems. Of particular concern are those systems where human actions are involved because these are novel to Earth's history. We have no prior experience of their consequences.

Fourth, climate disruption may cause a significant loss of biodiversity. Until recently, models of this outnumbered empirical studies. Now many ecologists are digging out old natural history surveys and repeating them. They should continue to do so. Many species are moving upslope or pole-ward and more studies will help elucidate which move, which do not and why.

Fifth, a striking omission is studies on how species respond to decreasing rainfall. As Figure 1 and Trenberth *et al*. [3] suggest, large areas of the planet show long-term drying trends, yet I am not familiar with comparable long-term studies that document the likely consequent loss of species.

Finally, there are many other ways in which species might become extinct other than by moving to ever-shrinking habitats. Importantly, we need to know whether species that do not move decline in abundance. 'Staying put' may be an even worse strategy than shifting one's range — but adequate documentation is scare.

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