

Essay

Predicting biotic responses to future climate warming with classic ecogeographic rules

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Models for future environmental change all involve global warming, whether slow or fast. Predicting how plants and animals will respond to such warming can be aided by using ecogeographic biological ‘rules’, some long-established, that make predictions based on observations in nature, as well as plausible physiological and ecological expectations. Bergmann’s rule is well known, namely that warm-blooded animals are generally smaller in warm climates, but six further temperature-related rules — Allen’s rule, Gloger’s rule, Hesse’s rule, Jordan’s rule, Rapoport’s rule and Thorson’s rule — are also worth considering as predictive tools. These rules have been discussed in the recent ecological and physiological literature, and in some cases meta-analytical studies of multiple studies show how they are applicable across taxa and in particular physical environmental situations.

Global temperatures are predicted to rise by ~1–5°C before the end of this century [1,2]. The observed 0.8–1°C warming since 1850 has already resulted in significant changes in animal phenology, range shifts and community structure [3–6]. Phenological changes include strong responses to warmer conditions in northern temperate zones, for example earlier breeding of birds and amphibians, earlier appearance of migrating birds and butterflies, and earlier flowering of plants in spring [4]. Geographic range shifts have been common, in which cool-adapted organisms have moved poleward as they track conditions favourable to their existence. Warm-adapted species also move poleward, appearing in temperate areas that would previously have been too cold for them. Community changes can involve the extinction of species in the tropics if they were close to their thermal tolerance limit before warming, as well as changes in predator–prey dynamics as species shift in and out of their former communities [6].

Although many predictions about biotic responses to future global warming have been derived from studies of temperature-related ecological, phenological, genetic and physiological responses [7,8], “scientists are still learning, making it difficult to make detailed climate-change predictions” [9]. A key question for biologists is how to use known

microevolutionary trends to predict the future in the face of a number of models for temperature increase.

This topic has interested biologists since the nineteenth century, when worldwide exploration stimulated interest in global biogeography, and scholars such as Humboldt, Wallace and Darwin saw the potential for synthetic conclusions about biogeography and ecology from numerous case studies [10]. As biologists mapped the occurrences of plants and animals across climatic zones, they noted certain shared properties of body size, appendage and organ ratios, colour, distribution ranges, and reproductive strategy. They encapsulated these observations in a series of ecogeographic rules (Box 1), many of which were named after their discoverers (Figure 1).

These ecogeographic rules were largely established as spatial descriptions of what we observe today and in the recent past (e.g. Holocene, Pleistocene), but they might be predictive of how organisms will respond to ongoing global change, and especially to rapid climate change, with a temporal perspective [11–13]. In this essay, we synthesise seven temperature-related biological rules that make detailed predictions about potential biotic responses to future climate warming. If it is accepted that these rules are valid, or at least correct within defined parameters, they can provide a

powerful predictive tool. We consider the rules in terms of the effects of temperature on body size, colour, appendages, organs, reproduction and distribution.

Body size

Temperature affects body size according to Bergmann’s rule, with larger body sizes in cold environments (higher altitudes and latitudes) and smaller body sizes in warm regions (lower latitudes) [14,15]. For example, invasive birds provide a perfect illustration of this rule, ranging from a minimum body mass of 54 g between 10–15°S, and increasing gradually to a maximum of 771 g between 55–60°S [16]. Such a pattern has been especially well documented in endotherms (birds and mammals) [17,18], while size-temperature patterns in ectotherms (e.g. arthropods, reptiles, marine molluscs) are much more complicated, showing different results according to the phylogenetic position of the groups and the geographic region occupied [19–21].

Many examples of body-size reduction with recent warming have been noted in diverse plants, fishes, birds, some terrestrial ectotherms, and mammals, with few opposites and some equivocal responses [22]. For example, the body masses of four passerine bird species in Israel show a 2–8 g decrease from 1955 to 2000 [23]. Fossil record data and modern laboratory experiments on marine animals revealed body size reduction of some marine taxa for past global warming and is likely to occur in future warming [24]. However, in seeking to predict trends of shrinking body sizes with future warming, the magnitude and direction of size responses may vary significantly, especially in ectotherms. The validity of Bergmann’s Rule is likely to be species-dependent rather than predictive at higher taxonomic level [19–21,23]. Although there is a need for theoretical models of size-dependent thermoregulatory and metabolic responses in order to predict size variations under climate warming, we can at least predict that endotherms and some ectotherms that follow Bergmann’s rule will show a reduction in mean body size as a result of future warming. Such responses could be achieved by



expansion of the numbers of smaller species or by a chronic shift towards smaller individuals within populations. Therefore, as a consequence of body size reduction, trophic networks and the structure and function of ecosystems will change substantially [22,25].

Colour

Gloger's rule states that birds and mammals should be darker in warm and humid equatorial environments compared to colder and drier areas [26]. This trend is driven by increases of melanins in many birds and mammals in humid, warm habitats [27]. How Gloger's rule operates through the prevalence of pigments requires a complex balance between temperature, humidity and latitude. The simple version of Gloger's rule is that all kinds of melanin in the skin increase with increasing temperature and humidity, although there is a 'complex' version of the rule in which the final colour depends on the balance between eumelanin, which gives black, dark brown and grey colours, and pheomelanin, which gives ginger and rufous colours [26]. Eumelanin prevails in wet conditions, and pheomelanin in dry conditions. However, at low temperatures, eumelanin and pheomelanin decrease, and organisms become paler, whatever the humidity [27].

In a survey of 271 case studies, the simple version of Gloger's rule was usually tested at the intra- or inter-specific level, providing evidence of darkening of colours as humidity rises: 82% of cases were explained by high humidity and 29.8% by high temperature [26]. So, perhaps the rule has to be modified to refer to humidity (dark when wet) rather than temperature, and it appears to apply to mammals, birds and insects [26,28]. It is worth noting that there are at least 26 case studies arguing against Gloger's rule [26]. Predicting the colour trends at high latitudes is much simpler, as precipitation at middle to high latitudes has been modelled to increase significantly with future global warming [1].

A recent global-scale study on 230 species of woodpecker supports the generality of Gloger's rule [29]. Further, temporal records of the brown morph

Box 1. Summary of ecogeographic rules.	
Rule	Major claim
Bergmann's rule	Larger body sizes are seen in colder environments (higher latitudes) and smaller body sizes in warmer environments (lower latitudes)
Gloger's rule	Animals living in humid and warm environments should be darker in colour than those in colder and drier areas
Allen's rule	Animals adapted to cold climates tend to have shorter body appendages (like limbs) than animals adapted to warm environments
Hesse's rule	Animals inhabiting cold environments have a larger heart in relation to body weight than closely related species inhabiting warm climates
Jordan's rule	Fishes can show an inverse relationship between water temperature and meristic characteristics such as numbers of fin rays or vertebrae
Thorson's rule	Benthic marine invertebrates at low latitudes tend to produce large numbers of eggs developing to pelagic, often planktrophic (plankton-feeding) and widely dispersing larvae, whereas at high latitudes such organisms tend to produce fewer and larger lecithotrophic (yolk-feeding) eggs and larger offspring, often by viviparity or ovoviviparity, which are often brooded
Rapoport's rule	Latitudinal ranges of plants and animals are generally smaller at lower latitudes (warm climates) than at higher latitudes (cold environments)

of the tawny owl in Finland show five significant increases over the 50 years up to 2010 [30]. It can be predicted at least that these animals, especially at high latitudes, will be darker in the future, driven by global warming. Where humidity increases in warm regions, organisms will likely become darker too. The darkening trend of mammals, birds and insects can significantly affect the geographic ranges of varied colour morphs, like owls in Finland [24,28]. Furthermore, the expansion of darker morphs at high latitudes will most likely lead to competition with the local light-coloured morphs.

Appendages

Body appendages, such as tails, feet and ears, of birds and mammals tend to be larger in warmer climates, an observation known as Allen's rule [31,32]. This can be seen in regional differences between modern human groups, with for example the maximum lengths of radius and tibia (longer arms and legs) increasing from the Equator to the Arctic [33]. In laboratory experiments, mice also exhibit strong positive correlations of ear area and tail growth with higher ambient temperatures [32].

Allen's rule has been confirmed widely among birds and mammals; for example, bill size in many birds increases with air temperature, perhaps as a means to dissipate excess body

heat [33]. In several Australian birds (parrots, cockatoos and crimson rosellas) bill surface area has increased 4–10% since 1871, related to post-industrial warming [34]. Further, in pairwise sister-species comparisons of 360 species of small mammals across the New World, their tails are predictably longer in the tropics [35]. The size of the foot and ear also showed similar latitudinal trends. In this study, there was no correlation of tail length with ambient temperature, but rather with latitude (closeness to the Equator), which might relate to the ecology of the small mammals and whether they are climbers or not and the nature of the evergreen forests they occupy [35]. This is an example of the generality of the classic ecogeographic rules, but it shows the need to track cause and effect to improve the predictability of responses to warming.

Allen's rule seems to apply widely among birds and mammals but requires further systematic testing [35–37]. Whether it is purely temperature-related (endotherms need larger appendages to dissipate heat in hot conditions) or sometimes related to ecological niches, requires more testing, although balancing thermoregulation cost during the breeding season with changing ambient temperature was proposed to be the mechanism driving Allen's rule [37]. Based on these tests, we predict

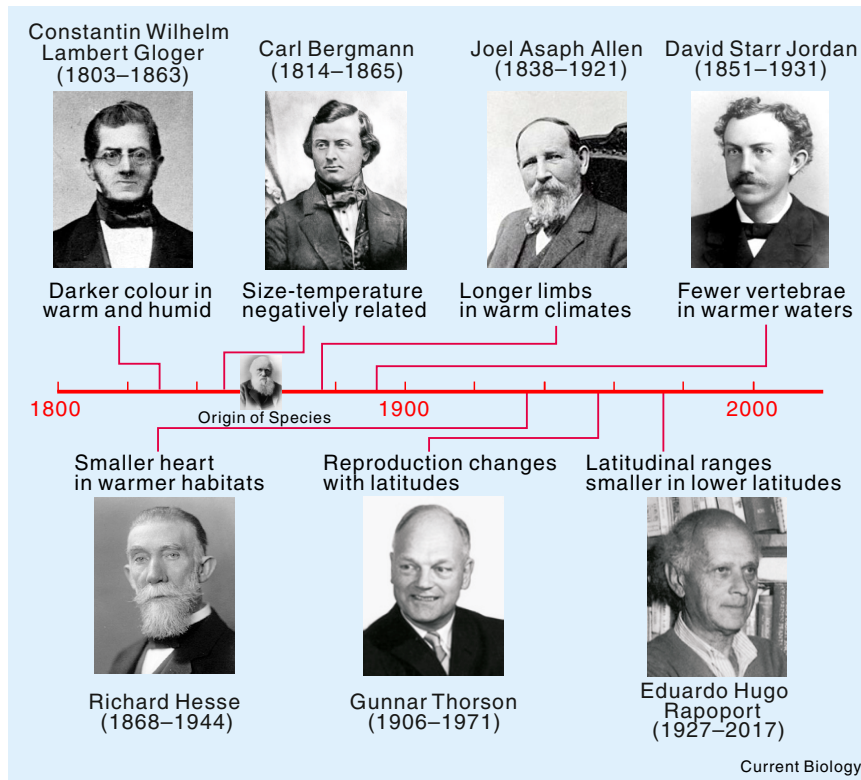


Figure 1. Timeline of ecogeographic rules.

The plot shows the date when the rule was enunciated, the person after whom it was named, as well as the publication of Darwin's 'Origin of species' in 1859.

that appendage sizes, such as ears and tails of small mammals, as well as bills of birds, are likely to increase with global warming.

Organs

Some organ proportions decrease with ambient temperature, following Hesse's rule, also known as the heart-weight rule [38]. For example, lung and heart weights of rodents showed 130–150% increase with a 3°C temperature reduction [38]. The explanation is that at cooler temperatures, endotherms such as mammals and birds have to work harder to maintain their body temperature, and hence the heart increases in size to pump more blood and the lungs increase in size to process more oxygen.

A second rule that relates to organ size and temperature is Jordan's rule, that there is an inverse relationship between water temperature and meristic characteristics (like numbers of fin rays or vertebrae) in various species of fish [39]. For example, the number of vertebrae in the galaxiid fish *Galaxias brevipinnis* positively

correlates with latitude, both in Australia and New Zealand [40]. In a study of a marine stickleback, *Gasterosteus aculeatus*, in North American coastal settings, not just numbers of vertebrae (total and caudal), but the numbers of dorsal- and anal-fin rays, increased in higher latitudes [41]. This relationship applies widely, but, like so many other rules, is complex and can depend on genetics and the environment during development [39]. In some cases, Jordan's rule may be a consequence of Bergmann's rule, that in cold climates, body size increases and with increasing body size in general, the number of vertebrae increases as well [42]. However, once vertebrae numbers begin to increase, those fish species show a higher tendency for the vertebral counts to vary with environmental influences, and simply to show higher variability within the population or species [39].

Allowing for the complexity of these rules, warming climates should lead to smaller hearts and lungs in mammals, as well as fewer vertebrae

and fin rays in fishes. These adaptive strategies will somehow prevent these animals from migrating to cooler habitats or going extinct, implying stronger resilience to temperature rises than equivocal responders. Therefore, particular conservation attention should be paid to species that do not follow Hesse's and Jordan's rules.

Reproduction

Reproduction can be affected by seawater temperature according to Thorson's rule: benthic marine invertebrates in warm areas tend to produce large numbers of eggs that develop into pelagic and widely dispersing larvae, whereas at high latitudes such organisms tend to have fewer and lecithotrophic (yolk-feeding) eggs and larger offspring, often produced by viviparity or ovoviviparity, and these are often brooded [43]. Observations of mussels and snails on the eastern North Atlantic shelf show significant increases of non-pelagic types with latitude, based on numerous observations [44,45]. A study of many crustacean species shows larger egg sizes at higher latitudes, and the same is seen for octopuses [43,46,47].

Thorson's rule had been applied exclusively to marine invertebrates, but evidence from butterflies has shown fewer and larger eggs at lower temperatures [48], and so the rule could be extended to terrestrial insects, as well as a few marine vertebrates, like fish. In a study across time, the small herring *Sardina pilchardus* increased egg abundance by 2–3 times during recent warming episodes [49]. Thus, the prediction is that global warming could drive many species of marine invertebrates, and possibly also some fishes and insects, to produce more and smaller eggs, as well as more marine benthic invertebrates with pelagic development. The reproductive adaptation revealed by Thorson's rule will lead to species diversity variations between adaptors and non-adaptors, and result in the extinction or removal of some species from a habitat [50].

Distribution

Rapoport's rule states that latitudinal ranges of plants and animals are

generally smaller at lower latitudes than at higher latitudes [51]. This pattern was first observed from distribution data of tetrapods, fishes, marine molluscs and trees, and it can be extended to elevational gradients, where taxa at high altitudes show larger ranges than at low altitudes [52,53]. This has been explained by the 'climatic variability hypothesis', that taxa originating in environmentally variable habitats, such as those at high latitude or high altitude, should evolve wider environmental tolerances and so can occupy larger ranges than taxa that, conversely, are adapted to more stable, and hence narrower, sets of environments at low latitude and altitude [51,54].

Observations show conflicting results. In one study on bumblebees [55], their southern limits shrank with increased warming, but their northern limits did not expand; so, as predicted by Rapoport's rule, their overall range size shrank with rising temperatures. In other long-term studies, however, range size has increased in the face of general global warming, but this is because many species' ranges have only shifted at high latitudes or high altitudes [56]. For significant poleward migrations and range expansions [3,5], the diversity peak also shifts to higher latitudes, and the absence of a tropical biodiversity peak implies that the tropics were already too hot as a result of rapid warming [57].

Rapoport's rule has been contested on the basis of criticisms of the statistical approaches and assumed underlying mechanisms [58,59]. Further, specific cases show how range size depends on more than latitude or altitude, but also on the geographic availability of suitable physical conditions for each species [51]. With global warming in the future, geographic ranges will move poleward, and the details of how this is achieved will differ among species: the poleward move might involve an increase in range size, or the range might stay the same or reduce as it moves. The fact that Rapoport's rule works sometimes and sometimes does not confirms the complexity of environmental drivers of ultimate range size; as temperatures rise, climates may become more variable

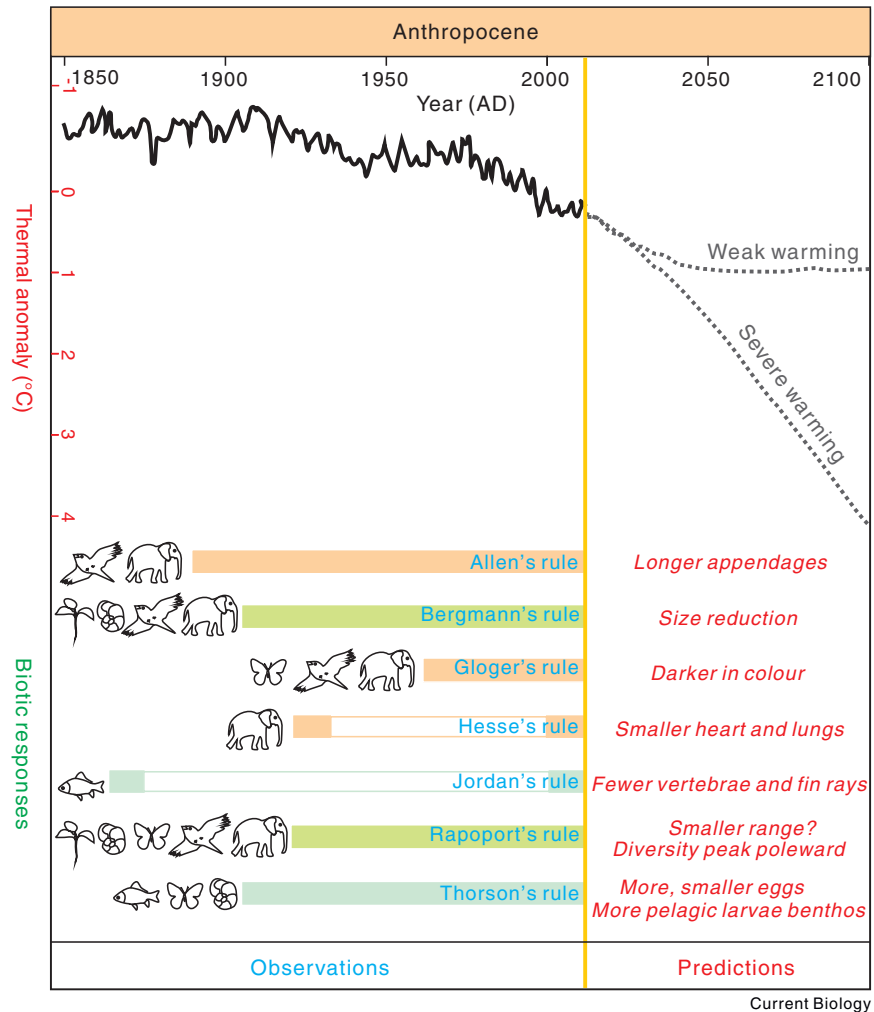


Figure 2. Predictions of potential biotic responses to future climate warming according to the ecogeographical rules.

The thermal anomaly curves are modified from global averaged combined land and ocean surface temperature change from 1850–2014 (solid curve) and modelled global average surface temperature change (dashed curves), both synthesized in the IPCC (2014). The key organisms for which each rule is known to apply (mammals, birds, plants, marine invertebrates, insects and fishes), as well as time scale over which case studies have been established, are indicated for each rule, together with a key prediction that might result from global warming. Solid bars indicate published data, blank bars indicate data gaps. Light blue for marine records, orange for terrestrial records and green for both marine and terrestrial records.

(e.g. warmer summers, colder winters), and so there will likely be different responses for each species.

Predictions and challenges

Although many ecogeographical rules have been disputed, new work to address methodological weaknesses in earlier studies has tended to find in favour of nearly all the rules cited here. Field and laboratory observations have shown how plants and animals respond to climate warming in terms of alterations to their phenology (earlier

breeding), geographic distribution (poleward shifts) and community structure [3–6,13,21–25,48]. The ability to generalise these observations depends on the ecological and physiological vulnerability of the organisms in question. The ecogeographical rules summarized above are no different.

We predict that global warming will result in many changes (Figure 2): reduced body sizes (Bergmann), darker colours (Gloger), larger appendages (Allen), smaller hearts (Hesse), and

Table 1. Quantified estimates of possible biotic responses to future climatic warming (quantified predictions under severe warming (rise of 5°C) are estimated to be 5 times the magnitude of rates for a 1°C rise in temperature, assuming these changes are correlated linearly).

Predictions	Observed changing rates (per 1°C rise)	Weak warming scenario (~1°C rise by 2100)	Severe warming scenario (~5°C rise by 2100)
Longer appendages	~0.5 mm in tail length of rat [32]; ~4–14% in bill surface of birds [34]	~0.5 mm in tail length of rat; ~4–14% in bill surface of birds	~2.5 mm in tail length of rat; ~20–70% in bill surface of birds
Size reduction	~116 g in mammals [61]; 14–27.2% in passerine birds [23]; 3–17% in plants; 0.5–4% in marine invertebrates; 6–22% in fish; 1–3% in beetles; 14% in salamanders [22]	~116 g in mammals (interspecific averaged); 14–27.2% in passerine birds; 3–17% in plants; 0.5–4% in marine invertebrates; 6–22% in fish; 1–3% in beetles; 14% in salamanders	~580 g in mammals (interspecific averaged); 70–136% in passerine birds; 15–85% in plants; 2.5–20% in marine invertebrates; 30–110% in fish; 5–15% in beetles; 70% in salamanders
Darker coloured morph at high latitude	0.15 frequency increase of brown tawny owl [30]	0.15 frequency increase of brown tawny owl	0.75 frequency increase of brown tawny owl
Smaller heart and lungs	8.5–12.5% in heart size of rodents [38]	8.5–12.5% in heart size of rodents	42.5–62.5% in heart size of rodents
Fewer vertebrae and fin rays	0.6 in fish vertebrae, 0.83 dorsal fin ray and 1.08 anal fin ray# [41]	0.6 in fish vertebrae, 0.83 dorsal fin ray and 1.08 anal fin ray#	3 in fish vertebrae, 4.15 dorsal fin ray and 5.4 anal fin ray#
More eggs	2–3 times in herring spawning [62]	2–3 times during herring spawning season	10–15 times during herring spawning season
Smaller eggs	0.94 mm in benthic octopuses [43]; 0.07 mm in fish egg [47]	0.94 mm in benthic octopuses; 0.07 mm in fish egg	4.7 mm in benthic octopuses; 0.35 mm in fish egg
More benthic species with pelagic larvae	~10% in marine gastropods# [45]	~10% in marine gastropods#	~50% in marine gastropods#
Smaller range	~0.42 km of bumblebees [55]	~0.42 km of bumblebees	~2.1 km of bumblebees
Diversity peak poleward	~140.8 km (likely the same with species poleward median speed [5])	~140.8 km?	~704 km?

Footnote: #: per 10-degree latitudinal decrease.

smaller geographic range sizes (Rapoport) in mammals and birds, fewer vertebrae in fishes (Jordan), and smaller eggs and more and more benthic species with pelagic larvae in invertebrates (Thorson). Referring to the known changes in some well-studied species, which followed these rules in the recent past, quantitative biotic changes are calculated, under the ‘weak warming’ and ‘severe warming’ scenarios, respectively (Table 1).

As we have summarised, there are many examples where responses to global warming are more complex than initially assumed in using these ecogeographic rules to predict biotic changes: species comparisons can be done pairwise within lineages, or phylogenetic comparative methods can be applied, where the trait values of all species under study are mapped on a phylogeny and hypothetical ancestral states considered [35,43]. These predictions can be sharpened by further work to determine how

physiology (e.g. ectothermic vs. endothermic), development, ecology (e.g. habitat complexity, role in food chain, body size), and genomics affect the outcomes [7]. Furthermore, as has been noted for nearly all ecogeographic rules, biologists have to disentangle the actual drivers of the trends — it may appear at first to be temperature, but humidity may also be critical on land, such as effects on colours of mammals and birds), while pH, salinity and productivity of seawater may also co-drive these predictions in marine organisms [1,60].

There have been many studies that predict biotic responses to future climatic warming as important data for species conservation [1,3–6,12–14]. Although the biotic changes predicted in this essay show no rigorous link to global biodiversity loss or other catastrophic bioevents, the consequences of these predictions may be important for understanding which species might survive and how

they might change. Lastly, many of these rules can be applied to humans: Bergmann’s rule, Gloger’s rule and Allen’s rule are valid in humans, while Hesse’s rule and Rapoport’s rule may well also be applicable. The validity of these predictions can, regrettably, be tested in the coming years.

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