

Shrinking body size as an ecological response to climate change

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Determining how climate change will affect global ecology and ecosystem services is one of the next important frontiers in environmental science. Many species already exhibit smaller sizes as a result of climate change and many others are likely to shrink in response to continued climate change, following fundamental ecological and metabolic rules. This could negatively impact both crop plants and protein sources such as fish that are important for human nutrition. Furthermore, heterogeneity in response is likely to upset ecosystem balances. We discuss future research directions to better understand the trend and help ameliorate the trophic cascades and loss of biodiversity that will probably result from continued decreases in organism size.

Climate change is a serious threat to Earth's ecosystems. Increased greenhouse gases and the associated rise in temperature have been implicated in melting glaciers, rising sea levels, acidification of marine and freshwater systems, increased ultraviolet-B radiation and increased fire frequency. The past century has seen a nearly 1 °C rise in global average temperature¹, with up to 7 °C of warming predicted by 2100 (ref. 2). Global warming has already led to significant shifts in the distribution, phenology and behaviour of organisms^{3–5}. Of 1,700 plant, insect, amphibian and bird species examined in a review by Parmesan and Yohe⁵, 80% had a poleward range shift of 6.1 km per decade, and 87% had an advancement in the timing of phenological events, such as breeding or flowering, of 2.3 days per decade. Such changes in distribution and phenology in response to climate change have received much attention in the literature, but only recently have studies begun to address the effects of climate change on development and growth. For many organisms, development and growth, and thus organism size, are affected by temperature and water availability^{6–8}. The increased temperatures and variability of precipitation associated with climate change are likely to influence the size of organisms, from primary producers to top predators^{9–11}. However, as we discuss below, the degree to which organism size is affected by temperature or precipitation variability is likely to vary within and between taxa, which could disrupt ecosystem functioning. Here, we briefly summarize the changes in organism size that are most likely a result of climate change and increased carbon dioxide levels, and theorize on reasons for the observed patterns of size declines. We present evidence from fossil records, experimental and geographic comparisons, and recent studies implicating current climate change in the shrinking size of organisms. We discuss the mechanisms that are most likely to be contributing to the observed patterns, exceptions to these trends and implications for biodiversity. Ultimately, our opinion is that this effect will become much more pervasive, and that research should focus on quantifying size trends more broadly, and identifying proximate and ultimate drivers of size declines.

Expanding lines of evidence

The sizes of numerous species have changed over time in relation to climate, and experimental evidence indicates that increased temperature and precipitation variability can reduce the growth rate and size of various organisms. So it is unsurprising that many organisms have become smaller as a result of anthropogenic climate change.

Fossil evidence. During past periods of global warming, both marine and terrestrial organisms became smaller. For example, soil burrows indicate that during the warming phase of the Palaeocene–Eocene Thermal Maximum (PETM), burrowing invertebrates such as beetles, bees, spiders, wasps, ants and cicadas shrank in size by 50–75% (ref. 12). Furthermore, diatoms, pocket gophers (*Thomomys talpoides*), California squirrels (*Spermophilus beecheyi*) and woodrats (*Neotoma* sp.) also shrank during past warming periods^{13–16}. Reductions in body size in fossils are particularly informative of what we can expect in the coming century, given that temperatures during the PETM, for example, increased by 3–7 °C and precipitation decreased by approximately 40%, similar to changes expected for many parts of the globe over the next century. Although current climate change is happening much more quickly than past periods of warming, the effect appears to be the same: smaller organisms with warmer temperatures. However, the rapid nature of current climate change may be partly responsible for the variable nature of the response, discussed below. Further studies on changes in size of fossil organisms could help quantify the expected change in size of organisms as a result of current climate change.

Experiments and geographic comparisons. A number of experimental and comparative studies also show that organisms are smaller when exposed to the conditions expected from climate change. For example, experimental acidification of water, an effect of increased atmospheric carbon dioxide, results in significantly reduced growth rates of calcifying organisms such as corals, scallops and oysters^{17,18}. Acidification also reduces the body volume of copepods, and can decrease coralline red algae mass by 250% (ref. 17). Collectively, these studies indicate that many calcifying species are likely to become smaller at a given age or completely lose the ability to form exoskeletons with continued climate change^{18,19}. Phytoplankton also have reduced growth rates in response to acidification²⁰, which could negatively affect all ocean life, because phytoplankton form the basis of the marine food web.

Experiments manipulating temperature have also shown that aboveground shoot and fruit biomass are 3–17% smaller for every degree Celsius of warming in a variety of plants (Supplementary Table S1)^{21–24}. Each degree of warming has also been shown to decrease body size by 0.5–4% in marine invertebrates^{8,10,25}, 6–22% in fish^{26,27}, 1–3% in beetles²⁸ and 14% in salamanders⁷ compared with controls. Comparative and experimental studies have also demonstrated the negative effects of drought and reduced precipitation on

Table 1 | Summary of size response to recent climate change.

Organism type	Negative response	Positive response	Equivocal response or no change	Example references
Plants	2	0	0	36, 37
Fish	8	3	2	10, 71, 72
Terrestrial ectotherms	3	1	0	38–40, 73
Birds	19	2	12	41–44, 74–78
Mammals	6	3	24	79–86
Total	38	9	38	

The table summarizes the number of species showing each type of response. Results are from an extensive literature search, including a search for 'mass' and 'climate change' (3,179 results), and 'size' and 'climate change' (4,316 results). Because these searches returned results that did not show changes in size or mass due to recent climate change, we pared the results based on relevance, judging by title and abstract, giving 30 results. We found additional studies by looking at the papers that cited those 30 results, and the relevant papers that were cited in each of those 30 results.

the size of organisms. Tropical trees^{6,29}, anurans^{30–32} and mammals³³ have all demonstrated decreased size or growth rate during drought years, under experimental drying conditions or along a decreasing precipitation gradient. Collectively, comparative and experimental studies indicate that a broad array of taxa are likely to get smaller with continued global warming, and that the rate and degree of shrinkage will vary widely.

Evidence implicating recent anthropogenic climate change.

Evidence of reduced organism size as a result of climate change over the past century has been reported in a number of studies¹¹ (Table 1). Plants were expected to get larger with increased atmospheric carbon dioxide, but their ability to use the extra carbon dioxide is dependent on temperature, humidity and nutrient availability^{34,35}. Over the past century, various plant species have shown significant negative correlations between growth and temperature³⁶, and positive correlations between precipitation and growth or seed mass, resulting in smaller grasses, annual plants and trees^{21,36,37} in areas that are getting warmer and drier.

Both aquatic and terrestrial ectotherms have been shrinking as well. Common toads (*Bufo bufo*) decreased in body size and body condition as temperatures rose 1.5°C over a 22-year period³⁸. In a meta-analysis of long-term surveys, experimental data and published results, Daufresne *et al.*¹⁰ demonstrated reduced body size of aquatic taxa related to increasing temperatures, for organisms that were subject to commercial harvesting and for those that were not. The consistency of their observed patterns emphasized the role of temperature in reduced body size, and they were among the first to suggest reduced body size as an ecological response to climate change. Furthermore, many reptiles have shown sensitivity to variation in rainfall, with tortoises (*Homopus signatus*) and marine iguanas (*Amblyrhynchus cristatus*) getting smaller with low precipitation^{39,40}.

Birds and mammals have also exhibited changes in body size with climate change. Various passerines, goshawks and gulls have all shown negative correlations between mass or wing length and temperature over the past half century (Table 1)^{41–44}. For mammals, the body mass of woodrats (*Neotoma* sp.), Soay sheep (*Ovis aries*) and red deer (*Cervus elaphus*) have all decreased significantly in response to warmer temperatures⁴⁵ and increasingly mild winters^{46,47}. In addition, polar bears have recently begun to decrease in size in response to reduced sea-ice extent^{48,49}. Although some exceptions to these patterns do exist (Box 1), further studies are likely to reveal numerous other examples of the negative effects of climate change on organism size.

Mechanisms of minimization

The explanations put forth for shrinking are diverse (Fig. 1). Numerous factors will lead to changes in organism size in relation to climate change, but we propose that the strongest responses will be due to two ecological factors, water and nutrient limitation, and

changes in ectotherm metabolic rate. We argue that because these factors are fundamental to the biochemistry of most organisms, some of the responses may be inescapable unless organisms rapidly evolve with a changing climate (Box 1). Over time, these ecological and other factors may lead to evolutionary responses favouring smaller individuals.

Terrestrial water and nutrient limitation. Plant growth is directly affected by water availability^{36,37}. Current climate models predict that most of the subtropics will get drier while much of the equatorial and high-latitude regions will get wetter². Moreover, many areas will experience higher variation in rainfall². Thus, even areas with increased rainfall will experience extended periods of water limitation. Reduced water availability will lead to decreased respiration and plant growth, and will in turn influence the size of consumers. To maintain body and population sizes, primary consumers will need to ingest larger quantities of smaller plants, and secondary consumers will need more prey items to maintain body size.

Soil nutrient levels are also likely to be altered by continued climate change. In areas that are predicted to get drier, fires will become more common. Fires result in high nitrogen loss⁵⁰, sometimes in excess of the replacement that accompanies fires through enhanced nitrogen fixation^{51,52}. Thus, the increased fire frequency in subtropical regions that results from higher temperatures and decreased rainfall can lead to excessive soil nitrogen loss. In turn, plant growth and net primary productivity (NPP) will decline, and the size of herbivores and carnivores could be indirectly reduced. In areas that are expected to get wetter, such as equatorial and high-latitude regions, increased precipitation can lead to nutrient loss owing to leaching⁵³. As with fire, loss of soil nutrients will result in reduced size of primary producers and possibly consumers.

Metabolism and the temperature–size rule. For ectothermic organisms, metabolic rates directly scale with temperature⁵⁴. Given a projected global warming of 1.1–6.4°C by 2100, Bickford *et al.*⁵⁵ predicted a 10–75% rise in metabolic rate for ectotherms. If all else remains equal, this increase in metabolism associated with climate warming will reduce the body size of ectotherms unless organisms can compensate with greater food intake or reallocating caloric resources. As organisms must divide energy between physiological maintenance, growth and reproduction, they might limit growth in favour of reproduction and basic maintenance physiology. Increased temperatures can also lead to smaller ectotherms by increasing developmental rate (termed the temperature–size rule⁵⁶). A smaller size results because growth rate does not often match the higher developmental rate that results from increased temperatures⁵⁷. Recent studies have shown a decrease in the size of ectotherms with warming (Table 1), suggesting that they are responding to increased temperatures with higher metabolism, quicker development and shrinking body sizes.

Evolutionary responses. Evolution will also play a role in shifting sizes. In some cases, smaller individuals are favoured by warmer or drier conditions, decreasing the mean size in a given population, as has already been observed in various taxa^{10,37,46,58}. Survival of small individuals can increase with warmer temperatures^{46,59}, and drought conditions can lead to smaller offspring³⁷, leading to smaller average size. In some cases, growth can also be limited by declining food and water resources, lowered NPP or reduced foraging area^{48,60}. As body size is often correlated with reproductive output, smaller individuals produce fewer or smaller offspring⁶¹. If smaller offspring are produced, a positive feedback loop might result, which would exacerbate the trend.

The tendency towards smaller individuals with increasing temperature is also favoured by Bergmann's rule, which predicts that endotherms should be larger in colder environments to conserve heat through thermal inertia⁶². Although Bergmann never mentioned the converse of smaller organisms in warmer environments, numerous studies have demonstrated that organism size does indeed decrease with increased temperature across latitudinal gradients^{63–65}. This probably explains some of the observed trends of shrinking organisms with increased temperatures resulting from climate change. Continued global warming is likely to favour smaller individuals, and we predict that organism size will continue to decrease over the coming century.

Upshots of down-sizing

The observed trends indicate that an increasingly wide array of taxa will get smaller in response to climate change, but that responses will be variable. Reductions in size are likely to be most pronounced in areas where climate change causes reduced precipitation coupled with warming. In these areas, NPP is likely to decrease, which will lead to reductions of resources across trophic levels and declining organism sizes for many species. Aquatic systems are also likely to see a decline in organism size owing to the reduced capacity of warmer waters to hold dissolved oxygen and nutrients. However, as noted above, the shift towards smaller size is not likely to be seen in all species, and magnitudes and rates of shrinking will be variable (Table 1).

Organisms with short generation times will probably respond rapidly to environmental changes, and observed size declines in species such as wild mustard, graceful warbler and white-throated woodrat might be responses to warmer or drier climates^{37,44,45}. Organisms with long generation times might not be able to respond rapidly enough for declines in body size to have been observed as of yet, and it is notable that there are relatively few examples of size changes in such organisms. It could be that these species are not decreasing in size, that data on size changes over time on such organisms are difficult to collect or that the responses of such organisms to environmental change is much slower. Further studies comparing size changes in organisms with short and long generation times will help determine the role of generation time in size reductions due to climate change. One extreme response to size reductions resulting from climate change is extinction. Organisms with narrow thermal tolerances and relatively small population sizes are likely to be at greatest risk. Ectotherms are likely to have increased metabolism with increased temperatures, which can lead to reduced body size if metabolic demands are not met. Furthermore, a reduction in the size of individuals makes them more susceptible to desiccation from evaporative heat loss⁶⁶, so ectotherms that are sensitive to desiccation, such as amphibians, may be the most susceptible to extinction resulting from size changes accompanying continued climate warming. Future research should examine such hypotheses to help determine which species are most at risk.

The variable magnitudes of change within species, coupled with variation in responses across taxonomic and trophic levels will probably upset ecological balances and community organization. For example, if all organisms were to shrink at the same rate and

Box 1 | Notable exceptions to the size-reduction trend.

Some exceptions to the pattern of shrinking body size have been observed, with studies reporting increased body size in certain fish, lizards, birds and mammals^{71,73,74,79,80,87,88} (Table 1). Many of these exceptions are from high latitudes, where increased growing or feeding seasons associated with global warming are likely to have pronounced effects. Although other organisms from high latitudes are decreasing in size (for example, Alaskan white spruce and polar bears^{36,49}), it is possible that patterns of shrinkage will be less common in areas where increased temperature and precipitation lead to increased net primary productivity. It is also important to note that many of the organisms that have increased in size are secondary consumers. Maintaining larger sizes might be difficult if prey species decrease in size or water becomes limiting owing to increasingly variable rainfall. Arft *et al.*⁸⁹ showed that although increased temperature led to initial increases in the growth of tundra plants, growth subsequently declined. Thus, initial increases in net primary productivity that result from warming at high latitudes might be short-lived, leading to reduced size of producers and consumers alike as climate change continues to increase in severity. Further studies on species that have become larger will indicate the mechanisms by which they have increased in size, and whether or not they will be able to maintain their increased size with continued climate change.

Some organisms might maintain their size or get larger because of their broad ecological niches. Predators with a diverse prey base, for example, might compensate for the smaller size of some prey items by shifting their diets to consume a larger proportion of bigger prey. Invasive and human commensal species are also likely to maintain their size because of their abilities to adapt rapidly in new or disturbed environments⁹⁰. The cane toad, *Chaunus marinus*, for example, can reach sexual maturity within 1–2 years, has a very broad diet and evolves quickly⁹¹. Although cane toads will experience increased metabolism with increased global temperatures, they could offset this with increased resource consumption from their broad prey base. Continued climate change might enhance selection for habitat generalists with extensive prey bases and wide thermal tolerances, ultimately favouring these invasive and human commensal species.

magnitude, then ecological interactions might not be adversely affected. Smaller predators could be sustained by smaller primary consumers, which could be sustained by smaller primary producers. However, observed response rates within and among taxa, and within and across trophic levels are highly variable (Table 1), which is likely to alter ecological interactions and disrupt ecosystem services. If producers shrink faster than consumers, then consumers are likely to suffer from a lack of resources that could reduce body condition, increase susceptibility to disease, lower birth rates and increase mortality. The results of any combination of these factors are likely to be reduced population size and increased susceptibility to extinction. If smaller species are favoured by continued climate change^{10,46}, larger species might be extirpated in areas most affected by climate change.

Changes in community composition can also alter nutrient cycling⁶⁷ and lead to changes in functional types, that is, shifts in the abundance of nitrogen fixers, or herbaceous versus woody plants. This has already been seen in the Amazon, where the proportion of lianas has increased, most probably because small, fast-growing lianas are able to take advantage of increased carbon dioxide levels better than large, slow-growing trees⁶⁸. Increased abundance of lianas is likely to negatively affect biodiversity, as lianas reduce tree

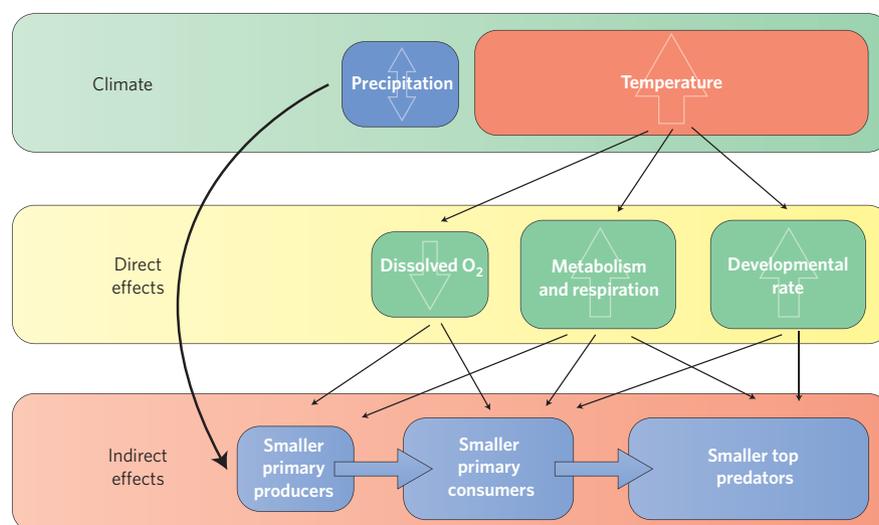


Figure 1 | Working hypothesis of the major processes of climate change effects on organism size.

growth and increase tree mortality, which reduces food, shelter and breeding space for other rainforest organisms. Further studies will indicate whether tree growth rates are reduced by increased liana abundance, which ecological interactions are negatively affected, and how ecosystem services might be affected as a result.

Marine systems are likely to suffer from variability in magnitude and rate of response as well. Phytoplankton with reduced growth rates owing to acidification²⁰ will support fewer or smaller marine consumers. Some calcifying organisms such as crabs and lobsters have been shown to increase in size with increased acidification, whereas others such as oysters and clams decrease in size²⁹. This variable response to acidification will probably upset marine ecosystem balances, and future research should examine the community-level effects of increased and decreased size of such organisms. Furthermore, warmer waters will negatively affect marine ectotherms in two ways: (1) increased metabolic rate is likely to reduce body size unless organisms can consume enough additional resources to meet their increased demands; and (2) decreased amounts of dissolved oxygen in warmer waters will make it difficult to meet increased metabolic needs. Future research could determine the net effects of increased temperature and reduced dissolved oxygen on metabolic demands.

Humans are also likely to be affected by shrinking organisms. For example, nearly a billion people rely on fish as their main source of animal protein, and fish are known or expected to decrease in size owing to climate change¹⁰, including farmed fish, crustaceans in aquaculture and fish from areas devoid of commercial fisheries^{1,26,27}. The combined effects of climate and fishing-induced reductions in size are co-occurring⁶⁹ and a much greater understanding is needed to assess the risk of further reductions in protein and calories from fish in the future. Crops will also be affected by climate change. Feeding the billions of additional people expected by 2050 (ref. 70) will become increasingly difficult as many areas become drier and crop plants are unable to grow as large. Water scarcity is predicted to reach alarming levels in areas with some of the highest population growth rates, such as South Asia⁷⁰. Even where annual rainfall averages remain unchanged, increasing variability in rainfall will make it more challenging to raise crops. If, for example, average rainfall remains the same or increases, but rain events become more concentrated in time, actual growing seasons of plants might decrease. Raising crops that depend on regular annual rains will thus become more difficult as increasingly long and frequent droughts result in more failed crop years.

Shrinking futures

Observed and expected patterns of decreased body size are widespread across different taxa, and are likely to be reported from an increasingly wide array of taxa over the coming century. Consequences of this shrinking are not yet fully understood, but could have far-reaching consequences for biodiversity and humans alike. Because recent climate change may be faster than past historical changes in climate, many organisms may not respond or adapt quickly enough. This implies that species may go extinct because of climate change. The species that can adapt are the species that will be affected by potential declines in body size. Future research should aim to identify the direct and indirect mechanisms responsible for observed size changes, quantify changes in size across a broad array of taxa using museum specimens, and examine the effects of heterogeneous size changes across trophic levels.

To understand the mechanisms, we encourage the use of both field and controlled laboratory experiments, as well as large-scale comparative studies of organisms already experiencing changes in natural areas. Studies of how the rate and magnitude of change in organism size differ in closely related species along environmental gradients will be the best systems to look for proximate drivers of the trend. An examination of a closely related group of organisms distributed along both elevational and latitudinal clines, and with historical data for comparison, would be an ideal starting point. These data may already exist from other studies on life-history variation, and could easily be examined for long-term changes in size.

Examinations of museum collections worldwide would allow for further quantification of the size-change trend. The majority of studies so far have focused on endotherms, but it is likely that ectotherms will show direct responses to increased temperature, for example. As ectotherms make up the majority of life on Earth, it is important to understand how these organisms are responding to climate change. Museum studies of ectotherms would require relatively little research funds, and can be carried out fairly quickly, and we encourage such studies to better understand the trend of size declines in response to climate change. Furthermore, museum studies are an excellent opportunity to examine the observed heterogeneity of size changes. Generation time may be an important factor in a species' response to climate change, and comparative studies of species with long and short generation times would help quantify the association between the magnitude of organism size change, extinction risk and generation time. Moreover, meta-analyses of existing

data would help quantify the relationship between generation time and size decline, as well as indicate which taxa remain understudied and in need of further attention.

Mesocosm experiments with primary producers (and known nutrient loads and solar inputs), primary consumers and at least two levels of predatory organisms can help illustrate how responses to increased temperature vary across trophic levels and how variable response rates across trophic levels affect ecosystem functioning. This modest complexity can also be realistically manipulated across climate variables (for example, temperature, precipitation, relative humidity and extreme climate events) and other environmental changes (for example, acid rain, nutrient variability and enriched carbon dioxide) to yield reliable information about natural systems. Modelling the importance and interactions of various environmental factors (above, coupled with climate change) can help identify the strongest drivers of size change for various organisms, and multi-model inference will enable more robust predictions of which organisms are likely to shrink, which are likely to increase in size and which might not change, across both taxonomic and ecological groups.

The consequences of shrinkage are not yet fully understood, but could be far-reaching for biodiversity and humans alike. Although there will be adaptive responses that natural selection will favour, ecosystem services and global ecological processes will most likely be altered, but not in ways that will benefit human livelihoods. Reduction in nutrients, food availability and water will probably have negative implications and are inter-related with climate change and shrinking organisms. Furthermore, extreme climate events might prove to be at the critical limit of some species' survival. We need to understand how and why organisms are shrinking, how feasible it is to mitigate or adapt to such climate change effects, and what it means for biodiversity and humanity if we are unable to change this pattern. Being able to predict change is critical in creating strategies that reduce negative effects and guide positive courses of action.

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