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COMMENTARY

Developmental phenotypic plasticity helps bridge stochastic weather events associated with climate change

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ABSTRACT

The slow, inexorable rise in annual average global temperatures and acidification of the oceans are often advanced as consequences of global change. However, many environmental changes, especially those involving weather (as opposed to climate), are often stochastic, variable and extreme, particularly in temperate terrestrial or freshwater habitats. Moreover, few studies of animal and plant phenotypic plasticity employ realistic (i.e. short-term, stochastic) environmental change in their protocols. Here, I posit that the frequently abrupt environmental changes (days, weeks, months) accompanying much longer-term general climate change (e.g. global warming over decades or centuries) require consideration of the true nature of environmental change (as opposed to statistical means) coupled with an expansion of focus to consider developmental phenotypic plasticity. Such plasticity can be in multiple forms – obligatory/ facultative, beneficial/deleterious – depending upon the degree and rate of environmental variability at specific points in organismal development. Essentially, adult phenotypic plasticity, as important as it is, will be irrelevant if developing offspring lack sufficient plasticity to create modified phenotypes necessary for survival.

KEY WORDS: Global warming, Ocean acidification, Developmental plasticity, Climate variability

Introduction – phenotypic plasticity studies typically focus on mature organisms and predictable experimental environments

Phenotypic plasticity in its many forms has been documented in detail for adult organisms (see Auge et al., 2017; Dewitt et al., 1998; Forsman, 2014; Gabriel, 2006; Ghalambor et al., 2007; Kelly et al., 2012; Lande, 2015; Moczek, 2010; Padilla and Savedo, 2013; Palacio-López et al., 2015; Pfab et al., 2016; Pigliucci, 2005; Pigliucci, 2009; Scheiner et al., 2017; Schneider and Meyer, 2017; Sultan, 2003; Voskarides, 2017). While beyond the scope of this Commentary to review this literature, phenotypic plasticity – encompassing molecular through to organismal levels – has been extensively studied and promoted as having an important role in organismal adaptation. Notably, phenotypic plasticity and the evolutionary advantages it may confer have been specifically highlighted in the context of climate change (e.g. Chevin et al., 2010; Fierst, 2011; Franch-Gras et al., 2017; Furness et al., 2015; Gomez-Mestre and Jovani, 2013; Mizutani and Kanaoka, 2017; Nunney, 2016; Parsons and Robinson, 2006; Reed et al., 2011, 2010; Rutherford et al., 2017). Many of these investigators have specifically argued a role for phenotypic plasticity as a mechanism

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for surviving climate change (though there has been more limited discussion of actual mechanisms by which this may occur).

Two aspects of arguments positing a role for phenotypic plasticity in surviving climate change require further scrutiny. The first issue is that climate change – whether anthropogenic or natural – is often viewed as a slow, inexorable environmental change – for example, the average global temperature increase or the decrease of the pH of oceans associated with increasing atmospheric CO_2. Experiments designed to investigate phenotypic adjustments associated with such environmental change are thus often based on average rates of change – for example, how do organisms respond to a 1, 2 or 5°C increase in temperature of their environment? – reflecting the predicted average changes over the next years or decades. Typically, such experiments monitoring phenotypic responses incorporate easily created steady-state increases in temperature. The problem with this approach as I see it is that many of the variables comprising climate change, especially as experienced in temperate terrestrial or freshwater environments, estuaries and marine pools and intertidal zones generally, can change in a rapid, even highly stochastic, fashion (e.g. Bokhorst et al., 2015; Drake et al., 2017; Kingsolver et al., 2011; Vitasse et al., 2014). Importantly, such environments in the short term almost never reflect the statistical average changes (e.g. an annual global temperature increase of small fractions of a degree Celsius). Rather, temperate terrestrial environments, freshwater environments, etc., often show fluctuating, extreme and unpredictable variations, which a statistical calculation of average values fails to capture. Here, I argue that the focus by investigators on annual global change rates, as undeniable and important as this, has unduly commandeered our perception of the dynamics of climate change.

The second shortcoming of discussions of the role of phenotypic plasticity in climate change is, I believe, an unbalanced focus towards the effects of climate change on end-stage, mature organisms rather than on their developmental precursors or, even better, the entire range of development. This is not to say that there hasn't been significant research on, as just one example, how ocean acidification affects larval forms of marine vertebrates and invertebrates (Esbaugh et al., 2016; O'Leary et al., 2017; Pistevos et al., 2017; Stiasny et al., 2016; Wang et al., 2017). However, an informal PubMed search revealed that studies of climate change and phenotypic plasticity (presumably in mature forms for lack of mention otherwise) outnumber similar papers that specifically mention 'embryos', 'larvae' or 'seedlings' by approximately 10 to 1. Yet, we know that developing organisms can be as, or more, susceptible than adult animals and plants to predictable or unpredictable changes in the environment (Burggren et al., 2017; Byrne et al., 2013; Croteau et al., 2008; Esbaugh et al., 2016; Kingsolver et al., 2011; Mueller et al., 2015; Müller and Rieu, 2016; Perrichon et al., 2017; Przeslawski et al., 2015; Radchuk et al., 2013; Reyna and Burggren, 2017).

Against this backdrop, this Commentary considers climate change in the context of developmental phenotypic plasticity. I

Glossary

Ambystomid
Various small- to moderate-sized salamanders of the genus *Ambystoma*.

Byssal fiber
Filaments secreted by bivalve mollusks to secure the shell to a solid substrate.

Critical window
A specific period during early development when organisms are particularly susceptible to environmental stressors.

Heterokairy
Plasticity in the timing of the onset of developmental events at the level of an individual or population.

Veliger
Final larval stage of some mollusks prior to permanent settling on the substrate.

first highlight the often variable and stochastic nature of climate and especially weather, before exploring the phenomenon of developmental phenotypic plasticity and its potential importance for surviving often extreme weather events associated with climate change.

Environmental change is complex and often unpredictable

Essentially, environmental variability reflects one or more of several general temporal patterns of climate and interposed weather events. It is important at the outset to differentiate 'climate' from 'weather', terms which are sometimes incorrectly conflated. As the American humorist Mark Twain commented: 'Climate lasts all the time and weather only a few days' (Le Row, 1887). More recently, and especially as climate change has accelerated and become a focal point, this view has become an aphorism among writers on climate change, usually presented as some variant on 'Climate is what you expect, and weather is what you get'. It is well recognized that climate generally, and climate change specifically, are highly layered phenomena, with many smaller, less obvious units hidden

within the whole (Lenormand et al., 2009; Saether and Engen, 2015; Stott et al., 2016). Variations in environment can occur over the long term (years or decades) or short term (days, weeks, seasons), and they can be either predictable or stochastic, as we will now consider.

The long-term view – climate

We know from geological evidence that the characteristics of the Earth's biosphere have changed radically over geological time (eras to eons). Fig. 1A indicates such a time course, using the schematic profile of atmospheric oxygen levels to indicate the extremely slow rate of change, even as levels themselves can vary greatly and in ways that can be explained after their occurrence but not predicted beforehand. Such changes actually are equivalent to or often exceed the time scale of evolution.

On a somewhat shorter time scale (e.g. years to millennia) we see clear rhythms of change with shorter-term stochastic events superimposed. Fig. 1B, for example, shows the schematic profile of global temperature over the last 400,000 years. Again, these long-term changes, even when unpredictable, may allow adequate time for natural selection and at least some evolution to occur.

Short-term environmental changes – weather intersects with climate

Some environments experience changes that, while potentially of high magnitude, are nonetheless quite predictable, e.g. seasonal changes. Fig. 1C shows schematic changes in environmental temperature over the course of a year. Generally, temperatures are lower in winter and higher in summer (a typical temperate climate), but weather events can intervene to create radical departures in expected temperatures. Indeed, during the 30 day period in the autumn (October) that I spent writing the first draft of this Commentary, air temperatures at my institution in Denton, TX, USA, varied between 9 and 38°C, with a single 20°C swing occurring in a 36 h period (Texas weather!). Then, as if the weather could be any more fickle, while revising this Commentary 2 months later in late December and early January, temperatures in Denton (which normally experiences very mild winters), fell to ~10°C below those in Moscow, Russia, as a record-setting cold temperature
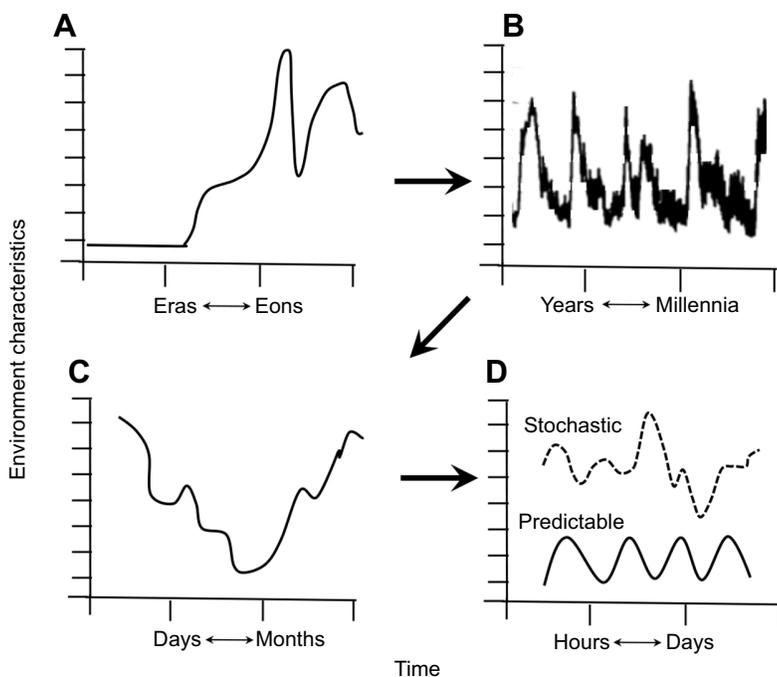

Fig. 1. Schematic representation of various patterns of environmental change in climate and weather. Environmental changes (*y*-axis) in any of temperature, oxygen level, rainfall, etc., associated with (A) climate change over geological time, in eons; (B) climate change over historical time in years to millennia; (C) climate change on an annual basis with superimposed shorter-term weather events; and (D) short-term weather patterns, which can be stochastic or highly predictable (e.g. ocean tidal events).

gripped continental North America and North-Central Asia reaped the benefit of the shift in the jet stream.

Even shorter-term changes on the scale of hours to days occur in many environments. Some of these changes are definitely not in the category of weather, but rather represent normal environmental cycling that is highly predictable; for example, the highly predictable, rhythmic changes in dissolved oxygen levels in small bodies of water with high daytime photosynthetic rates and high night-time respiration rates (Fig. 1D, Predictable). The partial pressure of oxygen (P_{O_2}) in such environments can range from 30 kPa during peak photosynthetic hours to near anoxia at night – swings in P_{O_2} that mimic daily vertical excursions in elevation far greater than those experienced by traveling from sea level to the summit of Mount Everest! Yet, these changes are consistent and predictable from day to day, with the baseline only slowly changing with season. Similarly predictable are the rhythmic changes in temperature, light, salinity, water availability, oxygen, etc., that intertidal organisms may experience on a typically near-twice daily basis.

In stark contrast to very short-term rhythmic and predictable environmental changes associated with tidal or diurnal cycles, temperate environments in particular experience short-term unpredictable changes in abiotic characteristics, e.g. changes in rainfall, temperature, wind, etc. (Fig. 1D, Stochastic) (Kingsolver et al., 2011; Schulte, 2014). This is clearly in the domain of 'weather', reflecting neither cyclic changes nor 'climate' per se (although a characteristic of a climate may be higher or lower degrees of variability from weather).

Typically, very short-term environmental variability, whether predictable or stochastic, is on a time scale far too rapid for adaptation through evolution to occur for most organisms. Of course, organisms may have adapted to environmental variability by evolving physiological, biochemical, behavioral or morphological specializations. Examples are ion transport isoforms in fish gills that operate over a large range of water salinities or isozyme families that span a larger temperature range in ectotherms.

Implications of climate and weather variability

As experimental biologists, we (and I include myself!) sometimes either forget or ignore the dynamic nature of many environments and instead focus on carefully stabilizing our experimental environments. Yet, we know (or should know) that natural environments are constantly changing, often in a highly unpredictable way. Experimental biologists also sometimes fail to make the important distinction between 'environmental change', which typically refers to short-term, sometimes unpredictable, changes in environmental factors (e.g. a cold front blowing in), and 'climate change', a common phrase referring to statistically averaged long-term, general and widespread changes in environmental factors (e.g. the recent global temperature increase). Consider the average annual global change in temperature contrasted with a 10 year running average and then contrasted again with the change over the entire twentieth century (Fig. 2). While the century average is 'only' a ~0.7°C increase, a global average temperature swing of nearly half of that amount occurred within just a few years at the mid-century mark. Breaking these data down by month would reveal even larger short-term temperature swings. And these are global averages. The short-term, non-predictable changes in temperature for specific temperate terrestrial and for many freshwater environments will be much larger. To emphasize the difference between mean and actual values, an organism can easily survive (or not even respond to) a statistically derived <0.1°C temperature increase per decade based
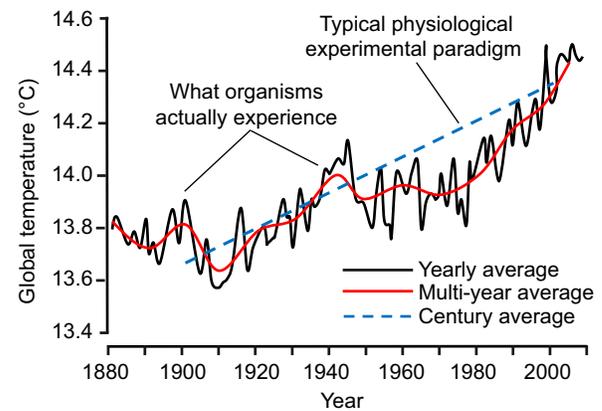

Fig. 2. Global temperature change (from 1880 to 2010) can be measured over different time frames and depicted in different ways, each leaving a different impression of the extent and rate of temperature change. Most physiological experiments exploring implications of global warming consider a change of a few degrees Celsius (taking the decades or century perspective), while fewer experiments consider the much larger, more stochastic temperature swings that actually represent what organisms experience over their individual life spans. See 'Implications of climate and weather variability' for additional discussion. Data from USA's National Oceanic and Atmospheric Administration.

on the global average increase, but that is small consolation when organisms fail to survive because the local environment is actually whipping back and forth by dozens of degrees Celsius in a few days or weeks.

Recognition of the highly variable nature of many environments has profound implications for experimental design. Increases in local variability in abiotic characteristics are advanced as one of the major short-term effects of global climate change (Karmalkar and Bradley, 2017; Pendergrass et al., 2017; Perkins-Kirkpatrick and Gibson, 2017). Yet, to focus briefly on just temperature, experiments are often designed to determine how organisms might survive global warming by incorporating an average 1, 2 or 5°C temperature increase. Reflecting this average, global view of global warming, papers increasingly appear with titles such as 'When could global warming reach 4°C?' (Betts et al., 2011) or 'Four degrees and beyond: the potential for a global temperature increase of four degrees and its implications' (New et al., 2011). The point is that, with the possible exception of subtidal marine environments (and even the surface temperatures of oceans can show great variation), a global increase of a few degrees is very likely to be predicated by far larger swings in temperature that may reduce fitness, if not prove lethal. Experiments incorporating large, and perhaps randomly changing, values are likely to be as or more insightful in terms of how organisms are going to cope with the local or regional implications of global warming. An excellent example of such a recent experiment involves the exposure of the intertidal limpet *Lottia digitalis* to combinations of both carefully regulated step-wise changes in temperature and also unpredictable temperature regimes during 2 week acclimation periods, followed by assessment of cardiac performance and biochemical mechanisms of tolerance (Drake et al., 2017). This study, which serves as an exemplar of the insight that can be gained from such experiments, demonstrated clear differences in physiological and biochemical indicators of stress between thermally predictable and unpredictable acclimation periods. Carrying out such experiments involving stochastic variation in ambient temperature, oxygen or other environmental variables is often technically far more demanding

than conducting traditional experiments of regulated, step-wise changes, and the analysis and interpretation of the resulting data can be complex. But, as the saying goes, that's not my problem!

To this point in the Commentary, I've discussed 'organisms', and the reader has likely imaged these as tall trees, large mammals or swimming fishes. I now turn to a population of organisms that may turn out to be the most vulnerable of all – developing organisms.

A short-term temporal context helps us understand how developing animals might cope with climate change
Developmental time and environmental variability
The fitness of developing organisms in a variable environment is affected by several factors, including the time course (length) of both the organism's development and the periodicity, magnitude and rate of change of environmental variation that occur during that plant or animal's development. Yet, in my opinion, such factors and especially their interactions are insufficiently investigated with regard to organismal fitness. To drive home this point with an extreme example, consider the bacterium *Escherichia coli*. Under ideal conditions, this bacterium divides every 20–30 min (Kubitschek and Woldringh, 1983; Wang et al., 2010), far too short a time to be influenced by typical environmental changes. Contrast that with development in the bullfrog (*Lithobates catesbeianus*), which, in northern parts of its range, can take as long as 3 years just to metamorphose from larva to adult frog. During their development, these bullfrog larvae can experience major unpredictable changes in everything from water temperature and oxygenation to predation pressure. I would argue that the capacity for developmental plasticity holds far greater relevance for the individual larval bullfrog, with its long pre-metamorphic development, than the bacterium, simply because of the enormous differences in developmental time and, thus, in the time for exposure to adverse environments.

I propose that the time required for development, relative to the rate of environmental change and its variability, can be an important factor when considering the contribution of developmental phenotypic plasticity to organismal fitness. Fig. 3 presents hypothetical 'fitness surfaces' that correlate with these various factors. If an organism's developmental time is brief, and its development occurs in a stable environment, then it could be argued that an organism may have higher fitness because of the lower likelihood of experiencing environmental stressors over its brief development time (depicted schematically in Fig. 3A). In contrast, longer developmental times could provide more opportunity for a developing organism to encounter environmental stressors, potentially reducing the organism's fitness, especially in a highly variable environment. Put (too) simply – the longer an organism takes to develop fully to maturity, the greater the chance that it will encounter unpredictable, extreme environmental stress that can affect its survival. Thus, organisms with both complex life cycles and long times to sexual maturity – e.g. redwood trees and Galapagos tortoises – are at greater risk from frequent and large environmental variability. It follows that factors that accelerate time for development (e.g. acutely but modestly increased temperature for plants and ectothermic animals) are thus more likely to help a developing organism avoid the deleterious effects of large and rapid environmental variability (Schulte et al., 2011; Sgrò et al., 2016). Essentially, such organisms will have 'developmentally outraced' potential variability in their environment. On the negative side, more rapid development may lead to reduced body size at maturity, so there may be fitness tradeoffs. However, an adult albeit of smaller size is at least in a position to reproduce, unlike an earlier developmental stage that failed to reach sexual maturity altogether.

It is interesting to speculate that developmental plasticity that enables acceleration of sexual maturity could be beneficial under certain environmental conditions. The movement forward of reproductive capability (or other traits) in the developmental plan, perhaps at the expense of other developmental processes or structures, is essentially the phenomenon of 'heterokairy' (see Glossary) (Mueller et al., 2015; Rundle et al., 2011; Rundle and Spicer, 2016; Spicer and Burggren, 2003; Spicer et al., 2011). Indeed, environmental influences (in addition to a 'simple' temperature increase) are presumed to accelerate behaviors, morphologies or physiologies necessary for reproduction in a wide variety of animals (Fuiman et al., 1998; Goldberg et al., 2016; Gomula and Koziel, 2015; Lewis et al., 2008; Mikolajewski et al., 2015; Norberg et al., 2001; Pishnamazi et al., 2014; Silberbush et al., 2015; Wańkowska and Polkowska, 2010) and plants (Dalling et al., 2016; Farnsworth et al., 1996; Silva et al., 2016) (Box 1).
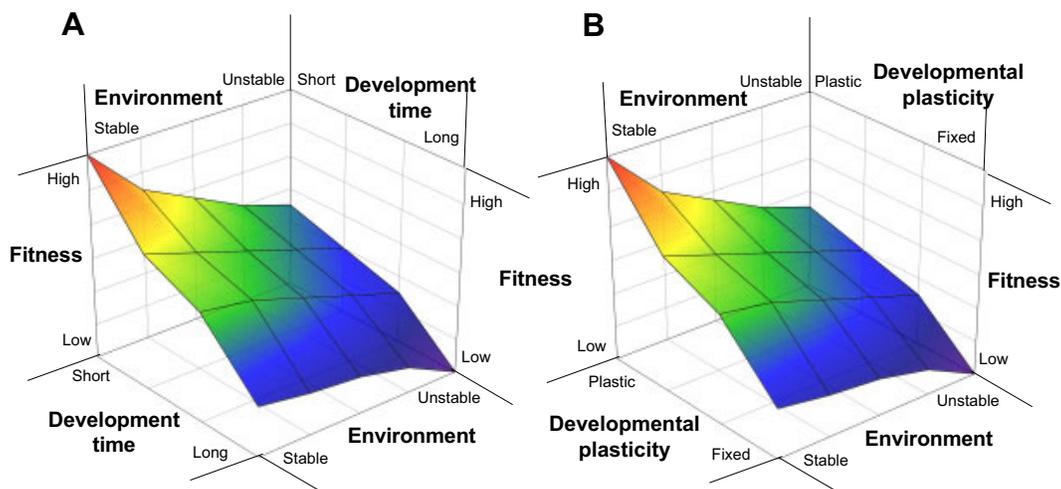

Fig. 3. Hypothetical interrelationships between environmental stability, fitness, time required for development and degree of developmental plasticity. In the face of unstable, highly variable environments, I propose that different organisms experience different levels of fitness according to (A) how rapidly they develop and (B) how developmentally plastic they are. Of course, different assumptions about the interactions of these factors will lead to different shapes of these fitness surfaces – empirical evidence to elaborate upon these relationships will be important to garner for future discussions.

Box 1. Case study of developmental challenges and environmental change
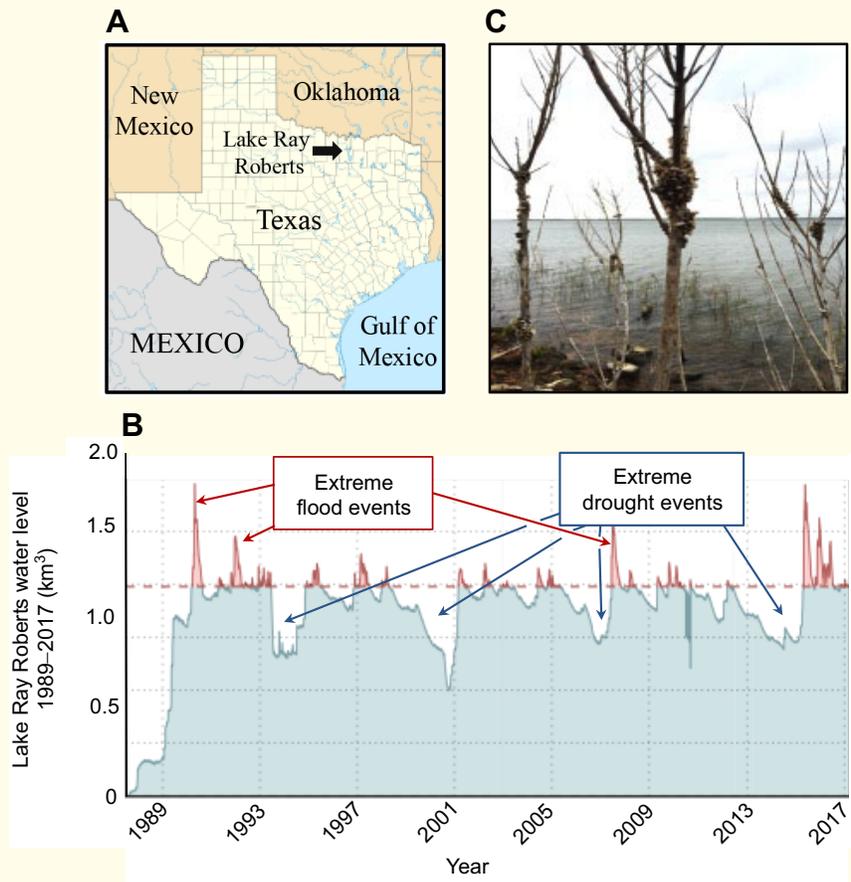
The race between achieving sexual maturity and surviving a rapidly changing environment is exemplified by the variable experiences of the veliger (see Glossary) of the zebra mussel (*Dreissena polymorpha*) in Lake Ray Roberts, a freshwater lake in north Texas in the USA (A). The water level in this man-made freshwater reservoir has varied near-randomly and rapidly over a 30 year period from initial reservoir filling in 1989 through to spring 2017 (B). In fact, lake water levels have rarely been in steady state, reflecting somewhat randomly alternating flood and drought weather events. Notably, agricultural and domestic water use have risen, but rather slowly and steadily and so do not substantially contribute to these short-term water level changes. Rates of water level change are as variable as the lake water level itself, with the rate of inundation of the lake shore by rising lake water levels typically being much higher (sometimes measured in just hours) than the rate of water level fall (weeks to months).

When shorelines are inundated by rising waters, the veligers of *D. polymorpha* will capitalize on this temporarily expanded range by settling on submerged tree limbs to begin their growth as sessile mollusks (B). Not only do the motile larvae of *D. polymorpha* have a greater horizontal and vertical range of settling surfaces during flooding events but they also experience greater variety in texture and composition of these surfaces. Settlement in some bivalves is highly limited by substrate (Carl et al., 2012). However, *D. polymorpha* show considerable plasticity during both the 2–3 week settling phase and subsequently during their 4–5 year adult life span, even modifying shell morphology and production of their byssal fibers (see Glossary) according to water velocity, temperature and water depth and substrate (Peyer et al., 2009). The plasticity of the settling response that allows larval settlement in flooded tree limbs certainly represents an advantage over bivalve species with larvae that are far more selective about settlement. Interestingly, morphological plasticity in seedlings of the amphibious plant waterwort (*Elatine* spp.) similarly provides for survival under varying degrees of habitat flooding (Molnár et al., 2015).

A key point is whether mussels attached to submerged tree branches can reach sexual maturity and actually reproduce before the water level inevitably recedes, exposing the mussels and killing them in place prior to gamete release (C). Thus, any factor that accelerates development could conceivably increase fitness of veligers in highly variable aquatic environments (see discussion of heterokairy in 'Developmental time and environmental variability', above). Image in B modified from Texas Water Development Board (https://waterdatafortexas.org).

Developmental phenotypic plasticity and environmental variability

Presuming that at least some modified phenotypes enabled by developmental plasticity are adaptive (see references in the opening paragraph of the Introduction), then high developmental plasticity may prove to be most beneficial to organisms encountering a high degree of environmental variation (Bateson et al., 2014; Peterson, 2012; Van Buskirk, 2002). This so-called adaptive plasticity hypothesis is developed in Fig. 3B. Noteworthy in this context is that stochastic environmental change can also arise from biotic factors such as food availability, competition and predation. When larvae of some ambystomid (see Glossary) salamander species are in an increasingly crowded and shrinking aquatic environment, a small, single-digit percentage of larvae are stimulated by environmental cues to transform into larger cannibalistic morphs

Table 1. Characterization of developmental phenotypic plasticity in developing organisms experiencing changing environmental stressors

	Characteristic of phenotype change	Timing and effect of environmental stressor during organismal development
Nature of occurrence	Obligatory	• When? Environmental stressor occurs during organism's developmental critical window.
		• Effect? Results in inevitable occurrence of phenotypic change (at least in short term, depending upon phenotype's reversibility).
	Facultative	• When? Environmental stressor occurs before or after developmental critical window.
		• Effect? Potentially results in modified phenotype whose value depends upon magnitude of environmental stressor and whether it triggers phenotypic change.
Value to organism	Beneficial	• Effect? Environmental stressor creates beneficial phenotypic modification.
		• Outcome? Aids survival through remainder of development. (Assumes no significant additional environmental change affecting survival until maturation.)
	Detrimental	• Effect? Environmental stressor creates disadvantageous phenotypic modification.
		• Outcome? Initially advantageous modified phenotype may become detrimental or lethal with yet another change in environment occurring during ongoing development (at least in short term, depending upon phenotype's reversibility).

with appropriate teeth, gut structure and jaw musculature. This extreme developmental plasticity allows them to survive by feeding on their siblings (Jefferson et al., 2014; Michimae and Wakahara, 2002; Walls et al., 1993). Again, developmental plasticity can enhance organismal fitness, especially when organisms inhabit a niche with high environmental variability (Fig. 3B).

An interesting issue pertaining to developmental plasticity is whether phenotypic changes occurring during development as a result of environmental stressors are actually reversible. A detailed discussion of this contentious topic is beyond the scope of this Commentary (for discussion, see Debat and David, 2001; Gabriel, 2005; Sommer et al., 2017; Woods, 2014). Certainly, those environmentally driven changes in phenotype occurring during so-called 'critical windows' (see Glossary) for development tend to be more lasting (and even permanent) compared with those occurring before or after this window (Burggren and Mueller, 2015; Burggren and Reyna, 2011; Daskalakis et al., 2013; Lloyd and Saglani, 2017; Senner et al., 2015). Whether a plant's or animal's phenotype is reversible or not may have implications for rapid environmental changes occurring in relatively slowly developing organisms, where a switched phenotype may only be temporarily advantageous.

Nexus of developmental time, plasticity and environmental variability
It is tempting to ascribe certain conventionally recognized characteristics to certain phases of developmental phenotypic plasticity, e.g. obligatory/facultative, deleterious/beneficial or even adaptive/maladaptive. However, I proposed that these typically distinctive views of developmental phenotypic plasticity can become conflated when considering a rapidly developing organism experiencing a highly variable environment (Table 1). Thus, in different populations of developing organisms experiencing different environments, the same modified phenotype derived from developmental phenotypic plasticity can be variously classified as unavoidable, facultative, detrimental or beneficial depending upon a combination of (1) when in development the environmental stressor occurs and (2) the presence/absence of the environmental stressor at later points in development. Clearly, our definition of developmental phenotypic plasticity has to be … well …. plastic itself!

Many investigators have evoked phenotypic plasticity as an important mechanism for survival in the face of climate change (for a small sample of studies and the perspectives they take, see Huey

et al., 2012; Kingsolver et al., 2011; Matesanz et al., 2010; Munday, 2017; Munday et al., 2017; Nicotra et al., 2010; Orizaola and Laurila, 2016; Reusch, 2014; Sgrò et al., 2016; Valladares et al., 2014; Vargas et al., 2017). Importantly, biologists studying phenotypic plasticity and climate change most frequently do so by considering plasticity in adults (e.g. Hetem et al., 2014; Matesanz et al., 2010; Sørensen et al., 2016; Stenlid and Oliva, 2016; Valladares et al., 2014). The role of phenotypic plasticity in the developing organism and how that contributes to coping with environmental change over multiple generations has been considered less frequently, despite numerous authors urging that adaptation to climate change be examined in the context of the full life cycle of an organism (Buckley et al., 2015; Burggren and Warburton, 2005; Kingsolver et al., 2011; Munday, 2014; Munday et al., 2017; Radchuk et al., 2013; Riek and Geiser, 2012; Seebacher and Grigaltchik, 2015; Slotsbo et al., 2016). The lack of greater focus on early developmental stages is unfortunate because these immature forms also experience shifts in environment/climate, just like their parents. Indeed, immature forms might actually be more vulnerable than adults to such shifts. Essentially, no degree of potential phenotypic plasticity – potentially so important as an adult – will ultimately matter if that organism never reaches adulthood. Thus, no development → no adult→no reproduction→no species survival!

Of course, due diligence requires pointing out that the reverse situation is true – phenotypic plasticity during development does not matter if the adult is insufficiently plastic to reproduce in the face of environmental change. My intent is certainly not to dismiss phenotypic plasticity in adults, nor to foolishly argue which developmental stage is more plastic or most benefits from this phenomenon. Rather, phenotypic plasticity in immature forms, especially when occurring outside of narrow critical windows in development, has the potential to counteract the potentially negative effects of stochastic environmental experiences. In essence, then, developmental phenotypic plasticity can help 'bridge' intermittent periods of adverse environments.

Concluding remarks: 'if you can't develop, you can't survive'
I have argued that a heavy focus on the stable, slow, inexorable components of climate change, with increases in global average temperature or oceanic acidification as the typical focus, has actually diverted the attention of physiologists, evolutionary

biologists and others away from the variable, extreme and stochastic components of, especially, temperate terrestrial and freshwater environments. Moreover, our perspective is perhaps limited by the additional focus on environmental effects of climate change on mature organisms, rather than their developing offspring. Phenotypic plasticity has frequently been evoked as an important mechanism for bridging climate change – rightfully so. However, we will derive an even greater understanding by adding a strong developmental component to our studies, as has been previously advocated (see Kingsolver et al., 2011; Radchuk et al., 2013).

I acknowledge that experiments on developing organisms with more-realistic short-term environmental changes (i.e. more 'weather' than 'climate') are more difficult to create, and the data more difficult to interpret, than typical contemporary experiments using steady-state protocols, often involving only adults. Yet, I reiterate that all the phenotypic plasticity an adult organism can potentially muster will be rendered irrelevant if that organism does not first reach sexual maturity! Given the frequently variable, even stochastic, nature of environmental changes (weather) associated with global climate change, the ability of a developing organism to switch to new phenotypes (and possibly reverse these switches) prior to adulthood might prove to be a vital component of bridging future climate change.

Finally, we need to go beyond 'just' documenting developmental plasticity phenomena to determining the actual mechanisms involved. This is very likely to include epigenetic components (e.g. Bräutigam et al., 2013; Burggren, 2016, 2017; Donelson et al., 2017) as well as genotype–phenotype interactions that are fixed in the genome through natural selection (Félix, 2016; Serobyan and Sommer, 2017; Susoy et al., 2015). Understanding such mechanisms could convert many of us from being observers/documenters of the effects on organisms of global climate change to being actual participants in anticipating and, perhaps, even combating the predicted outcomes.

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