

# Non-genetic inheritance and changing environments

## Abstract

Climate change continues to impact species worldwide. Understanding and predicting how populations will respond is of clear importance. Here, we review a mechanism by which populations may respond rapidly to these changes: Trans-Generational Plasticity (TGP). TGP exists when the environment experienced by the parents affects the shape of the reaction norm in their offspring; that is, the parental and offspring environments interact to determine the offspring phenotype. We survey 80 empirical studies from 63 species (32 orders, 9 phyla) that demonstrate TGP. Overall, TGP is taxonomically widespread and present in response to environmental drivers likely to be impacted by climate change. Although many examples now exist, we also identify areas of research that could greatly improve our understanding of TGP. We conclude that TGP is sufficiently established both theoretically and empirically to merit study as a potential coping tactic against rapid environmental changes.

## Keywords

Transgenerational plasticity • Maternal effect • Inter-generational • Cross-generational • Acclimation

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## Introduction: Organisms in A Changing World

Climate change has and will continue to impact species worldwide [1]. The environmental variables characterizing this change include mean temperature [2], extreme temperature [3], unpredictability in temperature [4], precipitation regime [5], and mean ocean pH [6]. Species will almost surely have to contend with altered food webs [7], the increasing threat of invasion [8], and variation in disease dynamics [9]. Evaluating how populations will cope with these changes is of considerable practical importance and will surely provide new insights about fundamental aspects of biology.

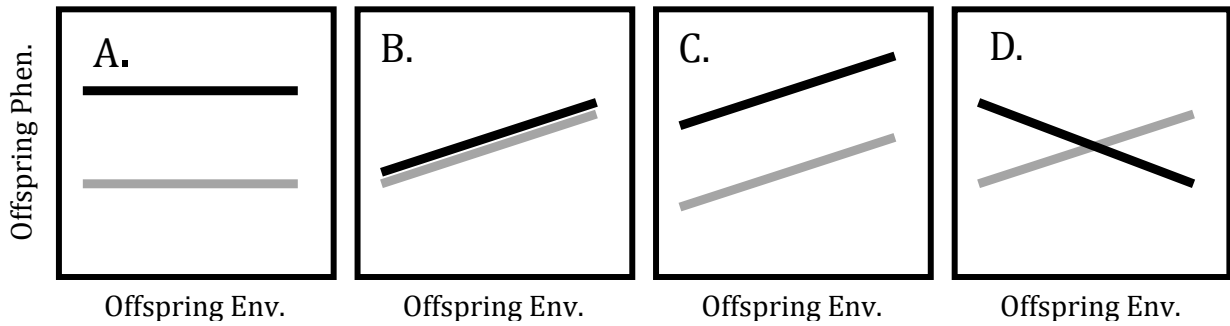
The focus of most work to date has been on migration out of stressful zones (e.g., [10]), within-generation phenotypically plastic responses (e.g., [11]), and evolutionary changes (e.g., [12]). Non-Genetic Inheritance (NGI) is another mechanism but has received comparatively little attention. Here, we review evidence for TransGenerational Plasticity (TGP) with respect to environmental variables likely to be impacted by climate change. Our goal is to use published reports to assess how common and taxonomically widespread TGP is as a phenomenon, in order to better assess its potential importance for coping with predicted changes in climate.

## Defining TGP

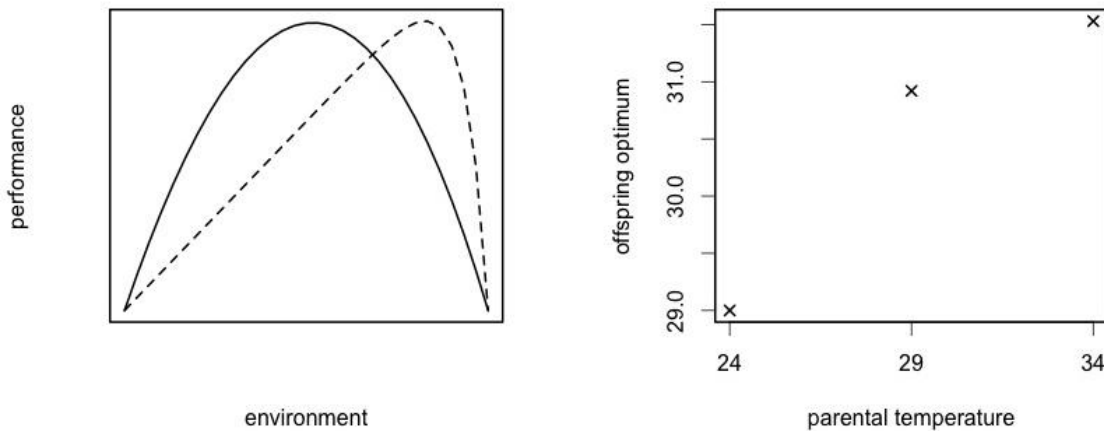
We use TGP to indicate instances in which the environment experienced by the parents affects the shape of the reaction norm in their offspring. In the simplest case, the parental environment and the offspring environment interact to determine the offspring phenotype (Figure 1). We make the distinction between TGP and the more generic term ‘maternal effects’ for two reasons. First, either parent may contribute to TGP (see below for specific examples). Second, TGP is only manifest when there is variation in the environment in both generations. The notion of TGP has appeared under various names, including maternal environmental effects [13], intergenerational effects [14], legacy or carry-over effects [15], cross-generational plasticity [16], and trans-generational acclimation [17].

For an additional characterization, we turn to the experiments of Salinas and Munch [18], who raised sheepshead minnows (*Cyprinodon variegatus*) for an entire generation in the laboratory at 21-22°C, then transferred individuals to 24, 29, or 34°C. They removed eggs quickly after females spawned and then measured the growth rates of the offspring in the same three temperatures. They showed that the offspring reaction norms depended upon the temperature that the parent experienced

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**Figure 1.** Maternal effects, plasticity, and TGP. In each panel, the vertical axis is offspring phenotype and the horizontal axis is the environment in which the offspring were raised. The black and grey lines indicate the responses when parents are held in two different environments. A) Pure maternal effects: the maternal (parental) environment influences the phenotype in a trait that exhibits no plasticity in response to the measured environment. B) Pure (within-generation) plasticity: the trait responds directly to the offspring environment, but is unaffected by conditions in the parent generation. C) No interaction: both parental and offspring environmental effects are present, but they contribute additively. Hence, plasticity is driven by the environment in both generations, but there is no effect that spans them both. D) TGP: the parental environment modifies both the elevation and slope of the offspring reaction norm. The outcomes of TGP are sufficiently different from either plasticity or evolution to merit its consideration separately.



**Figure 2.** A) In ectotherms, the temperature (x-axis)-growth rate (y-axis) relationship is a domed function. TGP is manifested by a shift in the offspring relationship based on the experience of the parent. B) The temperature for optimal growth of sheepshead minnows [18] depends upon the temperature that their mother experienced.

([18], Figure 1). Since sheepshead minnows are ectotherms, they have a temperature-growth rate profile that is dome-shaped (Figure 2A; see [19] for another example). In Figure 2B, we show, based on the data in Salinas and Munch [18], how the peak in the temperature-dependent offspring growth rate was influenced by the temperature the parents experienced: offspring whose parents experienced warmer temperatures have a temperature-dependent growth rate that peaks at a higher temperature.

### Empirical Evidence for TGP

Due to their limited movement and strong autocorrelation between parent and offspring environments [13], it was previously thought that TGP would be most prevalent in plants. However, as Figure 3 amply demonstrates, evidence for TGP is taxonomically widespread, with examples of TGP spanning 63 species, 32 orders, and 9 phyla. This is also true when we consider environmental variables likely to change due to

climatic processes (Figure 3, Table 1). Given this taxonomic breadth, TGP should be considered as a potential mechanism alongside migration, within-generation phenotypic plasticity, and adaptation by which organisms can respond to changing environments.

In constructing Table 1, we focused exclusively on cases where TGP was shown or thought to be adaptive, even though that is not necessarily always the case [20]. Table 1 includes species in which the parental environment may be confounded with the gestational environment. This adds a layer of complexity, although it is possible to test for TGP in internal fertilizers with a proper experimental design [21]. Given the many names that TGP-like phenomena have received over the years, Table 1 is surely incomplete.

Table 1 reveals some common features of species and the environments they occupy when exhibiting TGP: i) strong autocorrelation in environmental conditions during the reproductive period of the parents that lasts into the early offspring larval and/

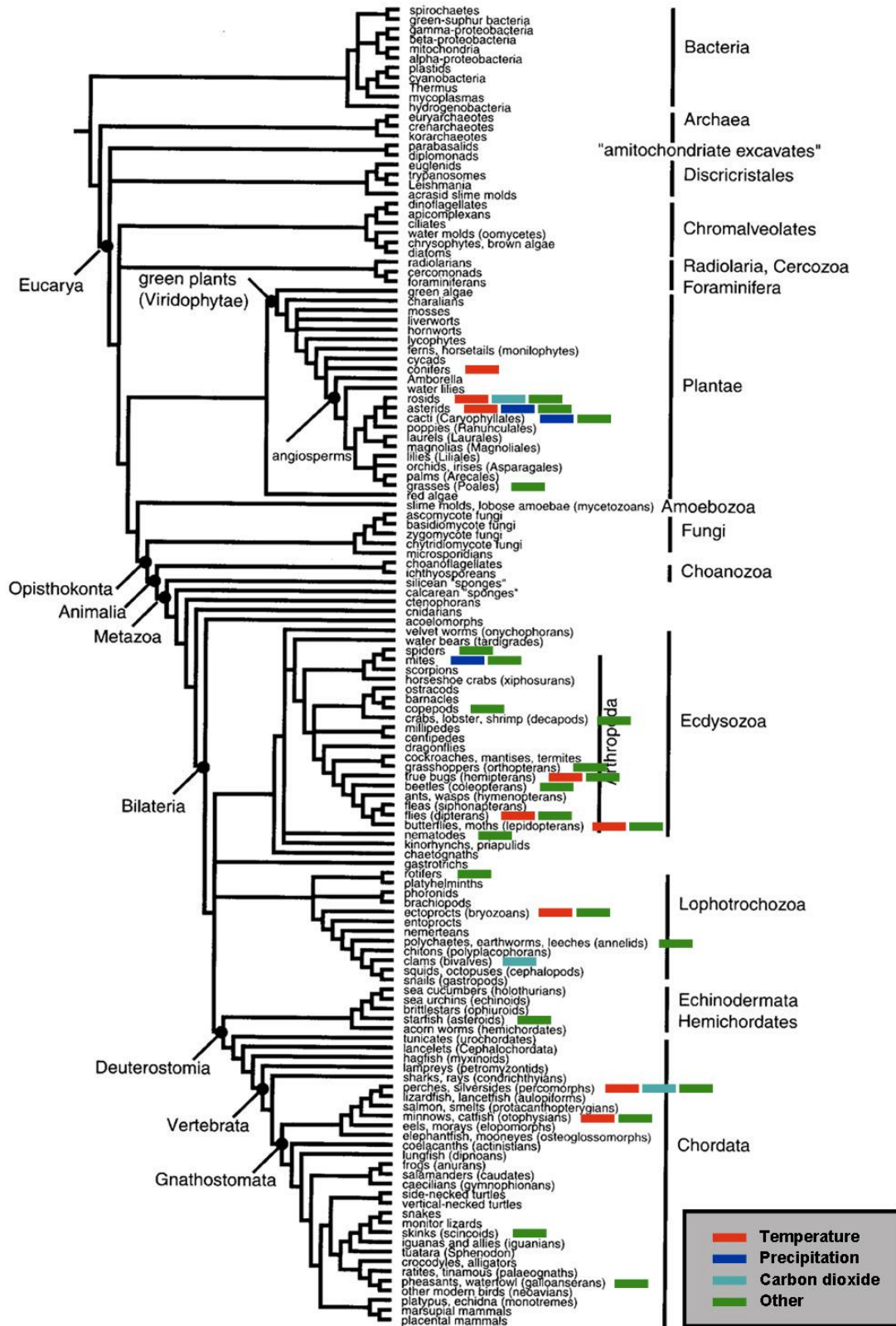


Figure 3. Species that exhibit TGP in response to various environmental stimuli (red = temperature, blue = precipitation, cyan = carbon dioxide, green = others) span many branches of the tree of life. [By permission of Oxford University Press, USA, ASSEMBLING THE TREE OF LIFE edited by Joel Cracraft and Michael J. Donoghue (2004) Ch. 34 "Assembling the tree of life: where we stand at the beginning of the 21st century" by Joel Cracraft and Michael J. Donoghue pp. 553-561, Figure 34.1 from p. 555 (adapted)].

Table 1. Studies reporting evidence of TGP. Species order within environmental stimulus follows the pattern in Figure 3.

Environmental variable	Trait(s)	Common name	Scientific name	Reference	Ref. number*
<b>TEMPERATURE</b>					
Mean temperature	Growth, timing of bud burst, freezing injury	Norway spruce	<i>Picea abies</i>	Johnsen et al. 2005. <i>New Phytol.</i>	[1]
Mean temperature	Germination rate, root growth, biomass, seed production	Thale cress	<i>Arabidopsis thaliana</i>	Blödner et al. 2007. <i>Plant Cell Environ.</i>	[2]
Mean temperature	Seed production	Thale cress	<i>Arabidopsis thaliana</i>	Whittle et al. 2009. <i>Botany.</i>	[3]
Heat stress	Number of rosette leaves and rosette diameter	Thale cress	<i>Arabidopsis thaliana</i>	Suter and Widmer. 2013. <i>PLoS ONE.</i>	[4]
Mean temperature	Tuber formation	Potato	<i>Solanum tuberosum</i>	Went. 1959. <i>Am J Bot.</i>	[5]
Mean temperature	Seed size, germination %, growth, age at maturation	Ribwort plantain	<i>Plantago lanceolata</i>	Lacey. 1996. <i>Evolution.</i> + Alexander and Wulff. 1985. <i>J Ecol.</i>	[6,7]
Mean temperature	Development time, age at maturation, growth	Milkweed bug	<i>Oncopeltus fasciatus</i>	Groeters and Dingle. 1988. <i>J Evol Biol.</i>	[8]
Mean temperature	Size, knockdown temperature	Fruit fly	<i>Drosophila melanogaster</i>	Crill et al. 1996. <i>Evolution.</i>	[9]
Mean temperature	Development time, pre-adult mortality	Yellow dung fly	<i>Scathophaga stercoraria</i>	Blanckenhorn. 2000. <i>Evol Ecol.</i>	[10]
Mean temperature	Larval time, pupal time, larval growth rate, egg size, pupal mass	Butterfly	<i>Bicyclus anynana</i>	Steigenga and Fischer. 2007. <i>J Thermal Biol.</i>	[11]
Mean temperature	Development time, hatchling lipid and protein content	Butterfly	<i>Bicyclus anynana</i>	Geister et al. 2009. <i>J Comp Physiol B.</i>	[12]
Mean temperature	Relative proportion of successfully metamorphosed larvae	Spiral-tufted bushy bryozoan	<i>Bugula neritina</i>	Burgess and Marshall. 2011. <i>J Exp Biol.</i>	[13]
Mean temperature	Vertebral and ray counts	Mangrove rivulus	<i>Rivulus marmoratus</i>	Swain and Lindsey. 1986. <i>Can J Zool.</i>	[14]
Mean temperature	Survival	Least killifish	<i>Heterandria formosa</i>	Travis et al. 1999. <i>Am Zool.</i>	[15]
Mean temperature	Growth	Sheepshead minnow	<i>Cyprinodon variegatus</i>	Salinas and Munch. 2012. <i>Ecol Lett.</i>	[16]
Mean temperature	Aerobic scope	Spiny chromis damselfish	<i>Acanthochromis polyacanthus</i>	Donelson et al. 2012. <i>Nature Clim Change.</i>	[17]
Mean temperature	Vertebral count	Zebrafish	<i>Brachydanio rerio</i>	Dentry and Lindsey. 1978. <i>Can J Zool.</i>	[18]
<b>PRECIPITATION</b>					
Drought stress	Biomass	Orange jewelweed	<i>Impatiens capensis</i>	Riginos et al. 2007. <i>Am J Bot.</i>	[19]
Drought stress	Root system growth, biomass	Redshank	<i>Polygonum persicaria</i>	Sultan et al. 2009. <i>Ecology.</i>	[20]
Drought stress	Survival	Redshank	<i>Polygonum persicaria</i>	Herman et al. 2012. <i>Integr Comp Biol.</i>	[21]
Relative humidity	Dehydration resistance	American dog tick	<i>Dermacentor variabilis</i>	Yoder et al. 2006. <i>J Insect Physiol.</i>	[22]
<b>CO<sub>2</sub></b>					
CO <sub>2</sub> concentration	Biomass	Blue lupine	<i>Lupinus perennis</i>	Lau et al. 2008. <i>Oecologia.</i>	[23]
CO <sub>2</sub> concentration	Development time, size	Sydney rock oyster	<i>Saccostrea glomerata</i>	Parker et al. 2012. <i>Global Change Biol.</i>	[24]
CO <sub>2</sub> concentration	Metabolic rate, growth, survival	Cinnamon clownfish	<i>Amphiprion melanopus</i>	Miller et al. 2012. <i>Nature Clim Change.</i>	[25]
<b>OTHER ABIOTIC VARIABLES</b>					
UV-C exposure	Level of homologous recombination	Thale cress	<i>Arabidopsis thaliana</i>	Molinier et al. 2006. <i>Nature.</i>	[26]

\*Please check list of Table references

continued Table 1. Studies reporting evidence of TGP. Species order within environmental stimulus follows the pattern in Figure 3.

Environmental variable	Trait(s)	Common name	Scientific name	Reference	Ref. number*
Salinity stress	Rosette diameter	Thale cress	<i>Arabidopsis thaliana</i>	Suter and Widmer. 2013. <i>PLoS ONE</i> .	[4]
Nutrient levels	Number of viable seeds	Redstem filaree	<i>Erodium cicutarium</i>	Jacobs and Lesmeister. 2012. <i>Funct Ecol</i> .	[27]
Light level	Seed mass, days to germination	American bellflower	<i>Campanula americana</i>	Etterson and Galloway. 2002. <i>Am J Bot</i> .	[28]
Light level	Rosette survival, adult survival, fruit number, seeds per fruit	American bellflower	<i>Campanula americana</i>	Galloway and Etterson. 2007. <i>Science</i> .	[29]
Nutrient and light levels	Seed mass, germination %, days to germination	American bellflower	<i>Campanula americana</i>	Galloway. 2001. <i>Am J Bot</i> .	[30]
Nutrient levels	Time to flowering, total biomass, total non-structural carbohydrate storage	Ribwort plantain	<i>Plantago lanceolata</i>	Latzel et al. 2013. <i>Oikos</i> .	[31]
Nutrient level	Total biomass	Blackseed plantain	<i>Plantago rugelii</i>	Miao et al. 1991. <i>Ecology</i> .	[32]
Nutrient level	Leaf weight, phosphorus concentration	Lamb's quarters	<i>Chenopodium album</i>	Wulff et al. 1999. <i>Can J Bot</i> .	[33]
Light and nutrient levels, soil moisture	Mass, emergence time, root length	Redshank	<i>Polygonum persicaria</i>	Sultan. 1996. <i>Ecology</i> .	[34]
Soil type	Photosynthetic rate, biomass	Barbed goatgrass	<i>Aegilops triuncialis</i>	Dyer et al. 2010. <i>Evol Appl</i> .	[35]
Salinity	Salinity tolerance, vigor	Sorghum	<i>Sorghum bicolor</i>	Amzallag. 1994. <i>New Phytol</i> .	[36]
Photoperiod	Resting egg production	Daphnia	<i>Daphnia pulex</i>	Alekseev and Lampert. 2001. <i>Nature</i> .	[37]
Copper exposure	Growth, size-specific heart beat rate	Daphnia	<i>Daphnia pulex</i>	Fernandez-Gonzalez et al. 2011. <i>Rev Chil Hist Nat</i> .	[38]
Copper exposure	Fecundity, survival	Intertidal harpacticoid copepod	<i>Tigriopus japonicus</i>	Kwok et al. 2009. <i>Ecotox Environ Safe</i> .	[39]
Copper exposure	Size, swimming time, copper resistance	Spiral-tufted bushy bryozoan	<i>Bugula neritina</i>	Marshall. 2008. <i>Ecology</i> .	[40]
Salinity	Survival to 8-cell stage	Serpulid polychaete	<i>Galeolaria caespitosa</i>	Tait et al. 1984. <i>Aust J Mar Freshw Res</i> .	[41]
Salinity	Development rate	Gray sea star	<i>Luidia clathrata</i>	Hintz and Lawrence. 1994. <i>Mar Biol</i> .	[42]
Contaminant exposure	Size, RNA:DNA	Mummichog	<i>Fundulus heteroclitus</i>	Nye et al. 2007. <i>Aquat Toxicol</i> .	[43]
Salinity	Growth rate, food conversion efficiency	Desert pupfish	<i>Cyprinodon macularius</i>	Kinne. 1962. <i>Comp Biochem Physiol</i> .	[44]
Cadmium exposure	Larval time to 50% mortality	Tilapia	<i>Oreochromis mossambicus</i>	Lin et al. 2000. <i>J Fish Biol</i> .	[45]
Copper exposure	Survival	Fathead minnow	<i>Pimephales promelas</i>	Sellin and Kolok. 2006. <i>J Fish Biol</i> .	[46]
Hypoxia	Time to loss of equilibrium	Zebrafish	<i>Danio rerio</i>	Burggren and Blank. 2009. <i>Sci Mar</i> . + Ho and Burggren. 2012. <i>J Exp Biol</i> .	[47,48]
Carotenoid level in diet	Hepatic carotenoid concentration	Chicken	<i>Gallus gallus</i>	Karadas et al. 2005. <i>Comp Biochem Physiol B</i> .	[49]
OTHER BIOTIC VARIABLES					
Predation	Seed mass, early plant growth	Radish	<i>Raphanus raphanistrum</i>	Agrawal. 2002. <i>Ecology</i> .	[50]
Support availability	Number of leaves	Twining vine	<i>Ipomoea purpurea</i>	Gianoli and Gonzalez-Teuber. 2005. <i>Plant Ecol</i> .	[51]
Predation	Leaf biomass	Ribwort plantain	<i>Plantago lanceolata</i>	Latzel et al. 2010. <i>Oikos</i> .	[52]

\*Please check list of Table references



continued Table 1. Studies reporting evidence of TGP. Species order within environmental stimulus follows the pattern in Figure 3.

Environmental variable	Trait(s)	Common name	Scientific name	Reference	Ref. number*
Predation	Leaf biomass	Hoary plantain	<i>Plantago media</i>	Latzel et al. 2010. <i>Oikos</i> .	[52]
Food availability	Recruitment, egg size, age and size at maturation, fecundity, survival	Soil mite	<i>Sancassania berlessei</i>	Plaistow et al. 2006. <i>Am Nat.</i>	[53]
Food quantity	Long-distance dispersal propensity	Lattice web spider	<i>Erigone dentipalpis</i>	Mestre and Bonte. 2012. <i>Behav Ecol.</i>	[54]
Food availability	Mode of reproduction	Daphnia	<i>Daphnia pulex</i>	LaMontagne and McCauley. 2001. <i>Ecol Lett.</i>	[55]
Food availability	Infection rate	Daphnia	<i>Daphnia magna</i>	Mitchell and Read. 2005. <i>Proc. R Soc B.</i>	[56]
Bacterial pathogens	Fecundity, age at maturation	Daphnia	<i>Daphnia magna</i>	Little et al. 2003. <i>Curr Biol.</i>	[57]
Cyanobacterial toxins	Fitness, time to maturity, time to first clutch	Daphnia	<i>Daphnia magna</i>	Gustafsson et al. 2005. <i>Ecology.</i>	[58]
Predation	Helmet length	Daphnia	<i>Daphnia cucullata</i>	Agrawal et al. 1999. <i>Nature.</i>	[59]
Conspecific density	Reproductive mode	Water flea	<i>Moina macrocopa</i>	Zadereev et al. 2003. <i>Aquat Ecol.</i>	[60]
Food quantity	Resting egg production	Water flea	<i>Moina brachiata</i>	Lopatina ad Zadereev. 2012. <i>J Siber Fed Univ.</i>	[61]
Food availability	Age at maturity, reproductive output	Springtail	<i>Folsomia candida</i>	Hafer et al. 2011. <i>Biol Lett.</i>	[62]
Predation	Immobility time, survival	Fall field cricket	<i>Gryllus pennsylvanicus</i>	Storm and Lima. 2010. <i>Am Nat.</i>	[63]
Conspecific density	Probability of being solitary, nymph coloration	Desert locust	<i>Schistocerca gregaria</i>	Islam et al. 1994. <i>J Insect Physiol.</i>	[64]
Host species	Fecundity, longevity	Pea aphid	<i>Acyrtosiphon pisum</i>	Via. 1991. <i>Evolution.</i>	[65]
Conspecific density	Proportion of alate morph	Milkweed-oleander aphid	<i>Aphis nerii</i>	Zehnder and Hunter. 2007. <i>Ecol Entomol.</i>	[66]
Diet type	Larval development time	Rove beetle	<i>Tachyporus hypnorum</i>	Kyneb and Toft. 2006. <i>Ecol Entomol.</i>	[67]
Bacterial pathogens	Antimicrobial activity in haemolymph	Mealworm beetle	<i>Tenebrio molitor</i>	Moret. 2006. <i>Proc R Soc B.</i>	[68]
Host type	Number of eggs laid	Leaf beetle	<i>Ophraella notulata</i>	Futuyma et al. 1993. <i>Oecologia.</i>	[69]
Diet quality	Development time	Australian neriid fly	<i>Telostylus angusticollis</i>	Bonduriansky and Head. 2007. <i>J Evol Biol.</i>	[70]
Food quantity	Egg-to-adult viability	Fruit fly	<i>Drosophila melanogaster</i>	Vijendravarma et al. 2010. <i>Biol Lett.</i>	[71]
Food quantity	Blood meal size, fecundity	Mosquito	<i>Anopheles stephensi</i>	Grech et al. 2007. <i>Malar J.</i>	[72]
Food quality	Phenoloxidase activity, haemocyte count, weight	Indianmeal moth	<i>Plodia interpunctella</i>	Triggs and Knell. 2012. <i>Funct Ecol.</i>	[73]
Host quality	Pupal mass, larval duration (males only), forewing length	Small heath butterfly	<i>Coenonympha pamphilus</i>	Cahenzli and Erhardt. 2013. <i>Proc R Soc B.</i>	[74]
Level of protein in diet	Larval mass	Small white butterfly	<i>Pieris rapae</i>	Rotem et al. 2003. <i>Ecol Entomol.</i>	[75]
Food availability	Fecundity, timing of reproduction	Nematode worm	<i>Caenorhabditis elegans</i>	Harvey and Orbidans. 2011. <i>PLoS ONE.</i>	[76]
Food quantity	Lifespan	Rotifer	<i>Brachionus plicatilis</i>	Kaneko et al. 2011. <i>Funct Ecol.</i>	[77]
Food availability	Age and size at maturation, egg size, hatchling size	Mangrove rivulus	<i>Rivulus marmoratus</i>	Lin and Dunson. 1995. <i>Ecology.</i>	[78]
Food availability	Juvenile size, male age at maturation	Guppy	<i>Poecilia reticulata</i>	Bashey. 2006. <i>Evolution.</i>	[79]
Level of protein in diet	Growth rate, sprint speed	Spotted skink	<i>Niveoscincus ocellatus</i>	Cadby et al. 2011. <i>J Exp Biol.</i>	[80]

\*Please check list of Table references

or juvenile stages, and ii) low dispersal relative to the degree of environmental heterogeneity such that offspring experience an environment similar to the parents' environment. These are precisely the theoretical conditions required for TGP to be advantageous [22] and are likely to occur in many species. Thus, we hypothesize that TGP is more common and widespread than previously thought.

In addition to manipulative experiments (such as those shown in Table 1), there is evidence suggestive of TGP in nature. For example, Hurst *et al.* [23] measured the thermal reaction norms of growth in three yearly cohorts of Pacific cod, showing that the cold-conditioned cohort came from a year in which anomalously cold conditions were present during the spawning period. While developmental plasticity in the offspring alone could also explain the observed differences in the cohort reaction norms (e.g., [24,25]), the temperature time series data does not rule out TGP since it demonstrates a link between parent and offspring environmental conditions. In Atlantic salmon, maternal early growth and condition at time of spawning influenced offspring growth and survival independently of egg size [26]. Obviously, it is difficult to unambiguously separate transgenerational from offspring within-generation phenotypic plasticity using time series data, so that manipulations of wild populations (e.g., [27]) may be the most reliable way of uncovering TGP in the field.

Temperature was the most common environmental variable used in TGP studies. This is not surprising: thermal regimes exhibit periods of strong temporal autocorrelation [28] and many taxa display a seasonal phenology in timing of reproduction. Temperature time series data from the field can therefore be a useful indicator for inferring the predictability of the parent-offspring environment when TGP is suspected. In laboratory experiments demonstrating thermal TGP in the larval and juvenile stages of a marine bryozoan, the parental temperature environment was well correlated with the offspring temperature environment for the duration of the early life-history stages affected [29]. In fact, Burgess and Marshall [29] showed that the temperature that mothers experienced was more influential on the dispersal potential of their offspring than was the temperature the offspring actually experienced (dispersal potential was higher in offspring from mothers reared in warmer water compared to mothers from colder water, contrary to expectations based on the temperature control of marine larval dispersal).

## TGP Can (and Should) Profoundly Alter Our Views of the Consequences of Environmental Change

The effects of environmental change on population dynamics are well documented [10,30]. In addition, TGP can play a large role in the dynamics of populations in time and space. For example, delayed density dependence was observed in soil mites exposed to different food environments as a result of transgenerational effects on various life history traits [14]. Effects were still observed after three generations [14], which can lead to highly complex population dynamics (e.g., [31]). Van Allen and

Rudolf [32] empirically confirmed that an interaction of previous and current habitat in *Tribolium castaneum* leads to very different patch carrying capacities and growth rates, thereby impacting meta-population dynamics. Dispersal, another key component of the dynamics of populations, can be easily influenced via TGP [29,33,34]. The ubiquity of TGP (Table 1) and pervasive effects on ecological dynamics implies that ignoring TGP is likely to lead to incorrect population projections.

As the environment changes, it will be critical to the persistence of populations to be able to track a moving fitness optimum. Bonduriansky *et al.* [22] reviewed modeling efforts of non-genetic inheritance, finding that this form of transmission can rapidly track fitness peaks, even in the absence of genetic variation (for an interesting possible counter-example, with epigenetics mediating the effects of inbreeding depression, see [35]). What happens once a population is close to the peak remains contentious. Moreover, not accounting for TGP in calculating heritability may lead to incorrect estimates, as the covariance between parents and offspring will be biased in the presence of TGP. This can, in turn, lead to erroneous predictions based on them. Any model of evolution under a changing climate that does not incorporate some form of non-genetic inheritance needs to be re-assessed given current knowledge.

## Future Research Directions

As with any emerging field, the excitement that followed the realization of strong TGP effects is now giving way to an abundance of questions. A number of these questions are relevant in assessing the role of TGP as organisms cope with climate change:

1. How predictable does the environment have to be? Key variables such as temperature will become more unpredictable in the future [4]. Hence, the correspondence between parent and offspring environment may be lost, depending on how long parents spend in assessing the environment and modifying the offspring's reaction norm. Knowing the length of this key imprinting period relative to the predictability of the environment could help assess whether TGP will be a coping mechanism or a maladaptive trait. In sheephead minnows, 7 days of exposure to a temperature is not enough to force a transgenerational effect, but 30 days is [18]. The study of anticipatory regulation [36-38] may also help in answering these questions.

2. What are the molecular mechanisms for transducing parental environments into heritable epigenetic variation? Molecular (e.g., whole methylome analysis) and experimental (e.g., demethylating agents) advances have already begun to answer this question. DNA methylation is the most common, but certainly not the only, method of transgenerational information transfer [39]; others include chromatin states, histone modification, and prions [40]. But in most cases, just how the environmental signal (e.g., temperature) results in variation in methylation profiles is unknown. Whether each mechanism acts differently (fidelity of replication, rate of epimutation, etc.) will have consequences to the long-term reliance of inherited variation.

3. How many generations are required for the non-genetic effects of the environment to be erased? Is there a reduced response after a few generations? In some cases, the environmental signal is lost after one generation while in others, multi-generation responses are evident [41]. This question is particularly relevant to population forecasting and when thinking of “genes as followers” in the process of adaptation [42].

4. How do phenotypic plasticity, TGP, and evolution interact? Non-genetic inheritance’s role within evolutionary theory needs to be properly assessed. The question of whether genes are followers or leaders in evolution, for instance, remains a contested one [43], although new approaches have been proposed to unify the various forms of inheritance (e.g., [44]). A sound theoretical and empirical synthesis—or, at least, a re-evaluation of the current one—is needed.

5. Are the trade-offs and costs involved in TGP the same as those identified for within-generation phenotypic plasticity [45,46]? Are there others that are inherent to the parent-offspring relationship? Who suffers the costs: parents or offspring [47]? How do traits that are modified

by the parental environment interact with other traits in the offspring [48]?

TGP appears to be taxonomically widespread. It is also sufficiently distinct, in terms of both ecological and evolutionary consequences, to merit study alongside migration, phenotypic plasticity, and evolutionary change as a mean of coping with climate change. Despite these conclusions, however, many questions remain, and we have tried to summarize some of them above. Better understanding of the mechanisms of TGP will help us predict how populations will respond to impending changes in the environment—perhaps the greatest challenge faced by evolutionary ecologists today.

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