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

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 sheephead 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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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/or 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.

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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* |
|-------------------------|---------------------------------------------------------------------------|-----------------------------------|---------------------|-----------------------------------------------|--------------|
| TEMPERENCE              |                                                                          |                                   |                     |                                               |              |
| Mean temperature        | Growth, timing of bud burst, freezing injury                              | Norway spruce                     | Picea abies         | Johnsen et al. 2005. New Phytol.              | [1]          |
|                         | Germination rate, root growth, biomass, seed production                   | Thale cress                        | Arabidopsis thaliana| Blodner et al. 2007. Plant Cell Environ.      | [2]          |
|                         | Seed production                                                          | Thale cress                        | Arabidopsis thaliana| Whittle et al. 2009. Botany.                 | [3]          |
| Heat stress             | Number of rosette leaves and rosette diameter                            | Thale cress                        | Arabidopsis thaliana| Suter and Widmer. 2013. PLoS ONE.           | [4]          |
| Mean temperature        | Tuberculosis formation                                                   | Potato                             | Solanum tuberosum   | Went. 1959. Am J Bot.                        | [5]          |
| Mean temperature        | Seed size, germination %, growth, age at maturation                       | Ribwort plantain                  | Plantago lanceolata | Lacey. 1996. Evolution. + Alexander and Wulff, 1985. J Ecol. | [6,7]        |
| Mean temperature        | Development time, age at maturation, growth                              | Milkweed bug                       | Oncopeltus fasciatus| Groeters and Dingle. 1988. J Evol Biol.      | [8]          |
| Mean temperature        | Size, knockdown temperature                                               | Fruit fly                          | Drosophila melanogaster| Crill et al. 1996. Evolution.               | [9]          |
| Mean temperature        | Development time, pre-adult mortality                                     | Yellow dung fly                    | Scaphophaga stercoraria| Blanckenhorn. 2000. Evol Ecol.            | [10]         |
| Mean temperature        | Larval time, pupal time, larval growth rate, egg size, pupal mass        | Butterfly                          | Bicyclus anynana    | Steigenga and Fischer. 2007. J Thermal Biol. | [11]         |
| Mean temperature        | Development time, hatching lipid and protein content                      | Butterfly                          | Bicyclus anynana    | Geister et al. 2009. J Comp Physiol B.       | [12]         |
| Mean temperature        | Relative proportion of successfully metamorphosed larvae                 | Spiral-tufted bushy bryozoan      | Bugula neritina     | Burgess and Marshall. 2011. J Exp Biol.      | [13]         |
| Mean temperature        | Vertebral and ray counts                                                  | Mangrove rivulus                  | Rivilus marmoratus  | Swain and Lindsey. 1986. Can J Zool.         | [14]         |
| Mean temperature        | Survival                                                                  | Least killifish                    | Heterandria formosa | Travis et al. 1999. Am Zool.                | [15]         |
| Mean temperature        | Growth                                                                    | Sheepshead minnow                 | Cyprinodon variegatus| Salinas and Munch. 2012. Ecol Lett.         | [16]         |
| Mean temperature        | Aerobic scope                                                             | Spiny chromis damselfish           | Acanthochromis polycanthus | Donelson et al. 2012. Nature Clim Change. | [17]         |
| Mean temperature        | Vertebral count                                                           | Zebrfish                          | Brachydanio rerio   | Denty and Lindsey. 1978. Can J Zool.         | [18]         |
| PRECIPITATION            |                                                                          |                                   |                     |                                               |              |
| Drought stress          | Biomass                                                                   | Orange jewelweed                  | Impatiens capensis  | Riggins et al. 2007. Am J Bot.              | [19]         |
| Drought stress          | Root system growth, biomass                                              | Redshank                          | Polygonum persicaria| Sultan et al. 2009. Ecology.                | [20]         |
| Drought stress          | Survival                                                                  | Redshank                          | Polygonum persicaria| Herman et al. 2012. Integr Comp Biol.       | [21]         |
| Relative humidity       | Dehydration resistance                                                    | American dog tick                 | Dermacentor variabilis| Yoder et al. 2006. J Insect Physiol.         | [22]         |
| CO2                     |                                                                          |                                   |                     |                                               |              |
| CO2 concentration       | Biomass                                                                   | Blue lupine                       | Lupinus perennis    | Lau et al. 2008. Oecologia.                  | [23]         |
| CO2 concentration       | Development time, size                                                    | Sydney rock oyster                | Saccostrea glomerata| Parker et al. 2012. Global Change Biol.     | [24]         |
| CO2 concentration       | Metabolic rate, growth, survival                                         | Cinnamon clownfish                | Amphiprion melanopus| Miller et al. 2012. Nature Clim Change.     | [25]         |
| OTHER ABIOTIC VARIABLES |                                                                          |                                   |                     |                                               |              |
| UV-C exposure           | Level of homologous recombination                                        | Thale cress                        | Arabidopsis thaliana| Molinier et al. 2006. Nature.              | [26]         |

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

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| Environmental variable | Trait(s) | Common name | Scientific name | Reference |
|------------------------|----------|-------------|-----------------|-----------|
| Predation              | Recruit, egg size, age and size at maturation, fecundity, survival | Soil mite | Sancassania berlesii | Piaistow et al. 2006. Am Nat. [53] |
| Food availability      | Long-distance dispersal propensity | Lattice web spider | Erigone dentipalpis | Mestre and Bonte. 2012. Behav Ecol. [54] |
| Food availability      | Mode of reproduction | Daphnia | Daphnia pulex | LaMontagne and McCauley. 2001. Ecol Lett. [55] |
| Food availability      | Infection rate | Daphnia | Daphnia magnä | Mitchell and Read. 2005. Proc. R Soc B. [56] |
| Bacterial pathogens    | Fecundity, age at maturation | Daphnia | Daphnia magnä | Little et al. 2003. Curr Biol. [57] |
| Cyanobacterial toxins  | Fitness, time to maturity, time to first clutch | Daphnia | Daphnia magnä | Gustafsson et al. 2005. Ecology. [58] |
| Predation              | Helmet length | Daphnia | Daphnia cucullata | Zadereev et al. 2003. Aquat Ecol. [59] |
| Conspecific density    | Reproductive mode | Water flea | Moina macrocopa | Lopatina ad Zadereev. 2012. J Siber Fed Univ. [60] |
| Food quantity          | Resting egg production | Water flea | Moina brachiata | Triggs and Knell. 2012. Funct Ecol. [61] |
| Food availability      | Age at maturity, reproductive output | Springtail | Folsomia candida | Hafer et al. 2011. Biol Lett. [62] |
| Predation              | Immobility time, survival | Fall field cricket | Gryllus pennsylvania | Storm and Lima. 2010. Am Nat. [63] |
| Conspecific density    | Probability of being solitary, nymph coloration | Desert locust | Schistocerca gregaria | Islam et al. 1994. J Insect Physiol. [64] |
| Host species           | Fecundity, longevity | Pea aphid | Acyrthosiphon pisum | Via. 1991. Evolution. [65] |
| Conspecific density    | Proportion of alate morph | Milkwed-oleander aphid | Aphis nerii | Zehnder and Hunter. 2007. Ecol Entomol. [66] |
| Diet type              | Larval development time | Rove beetle | Tachypterus hypnorum | Kynne and Toft. 2006. Ecol Entomol. [67] |
| Bacterial pathogens    | Antimicrobial activity in haemolymph | Mealworm beetle | Tenebrio molitor | Moret. 2006. Proc R Soc B. [68] |
| Host type              | Number of eggs laid | Leaf beetle | Ophraella notulata | Futuyma et al. 1993. Oecologia. [69] |
| Diet quality           | Development time | Australian neris fly | Telostylinus angusticollis | Bonduriansky and Head. 2007. J Evol Biol. [70] |
| Food quantity          | Egg-to-adult viability | Fruit fly | Drosophila melanogaster | Vijendravarma et al. 2010. Biol Lett. [71] |
| Food quantity          | Blood meal size, fecundity | Mosquito | Anopheles stephens | Grech et al. 2007. Malar J. [72] |
| Food quality           | Phenoloxidase activity, haemocyte count, weight | Indianmeal moth | Plodia interpunctella | Triggs and Knell. 2012. Funct Ecol. [73] |
| Host quality           | Pupal mass, larval duration (males only), forewing length | Small heath butterfly | Coenonympha pamphilus | Cahenzli and Erhardt. 2013. Proc R Soc B. [74] |
| Level of protein in diet | Larval mass | Small white butterfly | Pieris rapae | Rotem et al. 2003. Ecol Entomol. [75] |
| Food availability      | Fecundity, timing of reproduction | Nematode worm | Caenorhabditis elegans | Harvey and Orbidans. 2011. PLoS ONE. [76] |
| Food quantity          | Lifespan | Rotifer | Brachionus plicatilis | Kaneko et al. 2011. Funct Ecol. [77] |
| Food availability      | Age and size at maturation, egg size, hatching size | Mangrove rivulus | Rivulus marmoratus | Lin and Dunson. 1995. Ecology. [78] |
| Food availability      | Juvenile size, male age at maturation | Guppy | Poecilia reticulata | Bashey. 2006. Evolution. [79] |
| Level of protein in diet | Growth rate, sprint speed | Spotted skink | Niveoscincus ocellatus | Cadby et al. 2011. J Exp Biol. [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[28]. 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 sheepshead 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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