RESEARCH REVIEW

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Transgenerational plasticity and climate change experiments: Where do we go from here?

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Abstract

Phenotypic plasticity, both within and across generations, is an important mechanism that organisms use to cope with rapid climate change. While an increasing number of studies show that plasticity across generations (transgenerational plasticity or TGP) may occur, we have limited understanding of key aspects of TGP, such as the environmental conditions that may promote it, its relationship to within-generation plasticity (WGP) and its role in evolutionary potential. In this review, we consider how the detection of TGP in climate change experiments is affected by the predictability of environmental variation, as well as the timing and magnitude of environmental change cues applied. We also discuss the need to design experiments that are able to distinguish TGP from selection and TGP from WGP in multigenerational experiments. We conclude by suggesting future research directions that build on the knowledge to date and admit the limitations that exist, which will depend on the way environmental change is simulated and the type of experimental design used. Such an approach will open up this burgeoning area of research to a wider variety of organisms and allow better predictive capacity of the role of TGP in the response of organisms to future climate change.

KEYWORDS
acclimation, adaptation, environmental predictability, maternal effects, non-genetic inheritance, paternal effects, phenotypic plasticity, selection, within-generation plasticity

1 | INTRODUCTION

Environmental conditions are shifting from their long-term averages and extreme climatic events are becoming more common due to anthropogenic climate change (Collins et al., 2013). Organisms may respond to changing climates by shifting their distributions, adapting to new environments or acclimating through phenotypic plasticity (Hoffmann & Sgrò, 2011; Munday, Warner, Monro, Pandolfi, & Marshall, 2013). Plasticity is likely to be especially important in enabling organisms to cope with fast-changing environments (Gienapp, Teplitsky, Alho, Mills, & Merila, 2008), as the potential for rapid genetic adaptation may be constrained under predicted climate change (Merilä, 2012). While plasticity often occurs in response to environmental conditions experienced within a generation, the conditions experienced in one generation can interact with conditions experienced by subsequent generations to influence performance, termed transgenerational plasticity (TGP). TGP might be especially relevant in understanding biological impacts of climate change because environmental change will persist across generations for nearly all species. If TGP is adaptive (although this may not necessarily be the case), it can buffer populations against the immediate effects of climate change and provide time for genetic adaptation to catch up in the longer term (Chevin, Lande, & Mace, 2010; Kopp & Matuszewski, 2014).

Parents can alter the phenotype of their offspring through a range of non-genetic or epigenetic processes. These effects have been referred to by a variety of names including TGP, non-genetic inheritance, anticipatory parental effects, carry-over effects and

intergenerational effects (Bonduriansky, Crean, & Day, 2012; Salinas, Brown, Mangel, & Munch, 2013; Uller, Nakagawa, & English, 2013). Traditionally, research has focused on non-genetic maternal effects to offspring traits (Mousseau & Fox, 1998), however, evidence is accumulating for paternally mediated effects (Crean, Dwyer, & Marshall, 2013; Hallsson, Chenoweth, & Bonduriansky, 2012; Shama & Wegner, 2014). Epigenetic transmission (e.g. RNA-mediated modifications, epigenetic marks and DNA methylation) enables both parents to influence their offspring's phenotype other than by the genes they pass on (Ho & Burggren, 2010; Jiang et al., 2013). Importantly, these non-genetic and epigenetic processes can be influenced by the environment, and thus provide a mechanism by which the parental environment can influence the performance of offspring. Currently, the term TGP is often used to include any non-genetic effects that are observed in the current generation which is associated with the exposure of a previous generation to a new environmental condition. However, this definition will incorporate TGP, parental effects, as well as effects due to the developmental plasticity of the current generation induced by early cellular exposure. Instead, the term TGP should be limited to describe differences in offspring phenotype that occur due to the interaction between the current generation and previous generation's environmental conditions (Salinas et al., 2013).

This review aims to highlight experimental areas that require greater understanding to reliably predict TGP as a means of responding to rapid climate change and to identify future research directions. Other reviews have detailed the extent of TGP (e.g. Salinas et al., 2013; Uller et al., 2013), the mechanisms by which it can occur (e.g. Bonduriansky & Day, 2009; Jablonka & Raz, 2009), and its evolutionary or adaptive nature (e.g. Herman & Sultan, 2011; Marshall & Uller, 2007). Our review is not meant to be an evaluation of existing theory, nor a comprehensive assessment of empirical studies conducted to date. Rather, our goal is to outline appropriate experimental approaches to improve the likelihood of detecting TGP when it exists, address key knowledge gaps in TGP research, and suggest methods to control for potentially confounding effects. In doing so, we hope to open up this burgeoning area of research to a wider variety of organisms and study systems so that generalisations can be more readily made. We first explore the relationship between TGP and three aspects of environmental change that might improve our ability to predict where and when TGP will occur in response to climate change: (1) environmental variability and predictability, (2) the timing of environmental cues and (3) the relative magnitude of environmental change. We then consider the importance of distinguishing TGP from other forms of plasticity. Finally, we discuss the ability to distinguish TGP from genetic effects in current experimental approaches, because both non-genetic and genetic inheritance will be essential to shaping the potential of populations to respond to future climate change. Since we are interested in TGP responses to climate change, we focus this review on studies that consider environmental conditions relevant to future climate projections (e.g. temperature, salinity, CO_2) rather than a complete exploration of parental conditions that can induce TGP (e.g. hormones, chemicals, predators).

2 | TGP AND ENVIRONMENTAL PREDICTABILITY

Phenotypic plasticity is traditionally defined as the capacity of a given genotype to render alternative phenotypes under different environmental conditions but is more broadly considered as environmentally induced phenotypic variation (Pigliucci, 2001). Phenotypic outcomes of plasticity can be positive, neutral or negative to adaptive potential (Marshall & Uller, 2007; Uller et al., 2013), and limitations to plasticity exist due to underlying genetic architecture (Ghalambor et al., 2015; Scheiner, 1993). Environmentally induced phenotypic variation is often divided into three main types: developmental, reversible (or acute) and transgenerational (Angilletta, 2009; Munday et al., 2013). Developmental and reversible plasticity both occur within a single generation (i.e. within-generation plasticity: WGP), whereas in TGP, the environment experienced by earlier generations interacts with the environment of the current generation to determine the phenotype (Agrawal, Laforsch, & Tollrian, 1999; Salinas et al., 2013). Variation in environmental conditions over space and time can produce uncertainty about the future environment that should influence when, if, and which type of plasticity is favoured (Angilletta, 2009; Reed, Waples, Schindler, Hard, & Kinnison, 2010). Consequently, the variability and predictability of environmental conditions, including daily and seasonal variation (Kingsolver & Huey, 1998), can influence the capacity to produce plasticity to future change (Burgess & Marshall, 2014; Herman, Spencer, Donohue, & Sultan, 2014; Leimar & McNamara, 2015).

Different types of plasticity are expected to occur under different combinations of environmental variability and predictability, yet they are not necessarily mutually exclusive (Angilletta, 2009; Herman et al., 2014; Leimar & McNamara, 2015). When environmental conditions vary between generations and parents can effectively predict their offspring's environment, TGP should be selected for (Herman et al., 2014). Alternatively, TGP is instead predicted to occur with temporal stability, allowing offspring to accurately utilise parental cues (Leimar & McNamara, 2015). In contrast, where the environment varies greatly and in an unpredictable manner between generations (e.g. marine organisms where juveniles disperse over large distances), parents could be expected to hedge their bets by producing offspring with a range of phenotypes (Marshall, Bonduriansky, & Bussiere, 2008), although empirical evidence for bet hedging is scarce (Simons, 2011). TGP and bet hedging can also occur in combination, as environmental variance is often composed of both predictable and unpredictable components, with the concurrent evolution of both plasticity and bet hedging expected (Simons, 2014). That is, diversified bet hedging may occur around the norm of reaction (WGP: Furness, Lee, & Reznick, 2015; TGP: Shama, 2015). The prevalence of bet hedging and extent of within-brood phenotypic variation in relation to climate change and TGP may be substantially underestimated, as the majority of studies to date only explore the average phenotype of offspring. Given that increasing climate variability is predicted to pose an even greater risk to species than directional climate change (Vasseur et al., 2014), it is important

to shift the focus away from a strictly mean phenotype perspective and also consider the role of phenotypic variance in future TGP studies, since selection may not favour the average offspring phenotype and instead may favour the extreme phenotypes of offspring produced. Consequently, a continued mean phenotype focused approach within TGP research could reduce our capacity to accurately forecast population responses.

While theoretical predictions for TGP depending on environmental variability and predictability exist, generalisations from empirical evidence are difficult because environmental predictability is rarely considered in climate change research (exceptions Burgess & Marshall, 2011; Shama, 2015; Table 1). A broad range of species that are expected to experience diverse levels of environmental variation naturally possess the capacity for adaptive TGP to environmental change (Table 1), yet, a recent meta-analysis found only weak evidence for adaptive anticipatory parental effects (Uller et al., 2013). This is not to say that adaptive transgenerational effects are weak, but rather, that we may not be looking at the right time points in the life history or using relevant cues of environmental change to promote TGP. For example, if the predictability of the environment is poorly characterised, and experimental manipulations of environmental cues are based on this, detection of TGP may not be possible even when it is present (Burgess & Marshall, 2014; Uller et al., 2013) Additionally, the type of environmental predictability can also influence phenotypic variation of future generations (Shama, 2017). Periodic fluctuations like seasonality or tidal cycles, with regularity in the timing and magnitude of changes around the average environmental state, may have very different effects on offspring phenotypes than stochastic environmental change (or environmental noise), whereby predictability is determined by the degree to which the environment is similar between successive time points (e.g. autocorrelation; Marshall & Burgess, 2015). It may be instructive to re-analyse Uller and colleagues' data with the addition of a variable that accounts for the environmental variation experienced by each of the species. In addition, it would be interesting to incorporate an understanding of the relative environmental quality offspring conditions offer. Engqvist and Reinhold (2016) eloquently highlight that offspring phenotypic expectations with TGP are not the same if the environment of parents and offspring do not interact additively (as is the case when, e.g. parents facing a good environmental condition greatly affect offspring phenotype when their offspring experience poor environments but do not markedly affect the phenotype of offspring in benign conditions).

Within the current review, we summarise the transgenerational outcomes, specifically whether the nature of the TGP response is positive or negative in relation to projected future climate change (see Table 1). From this data, we explore the proportion of cases that found evidence for positive, potentially adaptive TGP, in the face of climate change compared to negative or no TGP effect. We found that the transgenerational response reported was positive in 42% of cases, 22% of cases were negative, and there was a neutral response in 36% of cases (Table 2). Looking in more detail, this pattern of transgenerational response did vary slightly between some of

the ecological groups, but this is likely to be influenced by the number of studies within each group (i.e. low number of studies on reptiles and amphibians). Interestingly, the number of observations for positive TGP response was higher in studies that applied environmental change cues outside of the normal seasonal conditions experienced (Table 2).

The difficulty with investigating the influence of environmental variation for most species is that there is not sufficient data on the microclimates that individuals experience, since most climatic data sets are compiled at a regional scale. Furthermore, in addition to limitations with measurement scale, non-sessile species can have access to a range of microclimates within their territory or residence area, and thus may not experience the average or full range of conditions measured. The level to which individuals behaviourally regulate the environmental conditions they experience can alter the plastic capacity of other traits including physiology and morphology (Buckley, Ehrenberger, & Angilletta, 2015; Hertz & Huey, 1981; Huey, Hertz, & Sinervo, 2003). Technology advancements (e.g. miniaturisation of archival and acoustic tags) does mean that for many organisms direct measurements of their microenvironment are becoming possible, however, it may never be an option for the majority of small and micro-organisms. The risk that exists within climate change experiments completed to date, where the focus has overwhelmingly been to apply average projected future changes with no consideration of the natural variation that should be simulated around it (exceptions include Dammerman, Steibel, & Scribner, 2016; Manenti, Sørensen, Moghadam, & Loeschcke, 2014 in relation to WGP; Shama, 2017 for TGP), is detecting higher levels of TGP than might actually occur in nature since plasticity would be expected to occur more readily when conditions are predictable. Future research would benefit from a greater focus on environmental predictability and variability, since determining plastic responses of species to future climate change requires experiments designed with an understanding of the environmental variation that naturally occurs in the study system and its predictability across generations (Vasseur et al., 2014; Vazquez, Gianoli, Morris, & Bozinovic, 2015).

3 | TIMING OF ENVIRONMENTAL CHANGE

The time during ontogeny at which an environmental change is experienced will directly influence both the phenotypic response within the individual (WGP) and the effects on offspring produced (TGP). Two life stages have been identified as critical periods when environmental conditions experienced by parents can influence the next generation: throughout early development (from fertilisation to early juvenile development) and prior to and during reproduction (Burton & Metcalfe, 2014; Fawcett & Frankenhuis, 2015; Feil & Fraga, 2012). Transgenerational effects are especially sensitive to experiences around conception or embryogenesis, because early embryonic cells are more sensitive to environmental influences and epigenetic changes during early development affect a higher proportion of cells (Burton & Metcalfe, 2014). Large effects during early life

TABLE 1 Studies exploring transgenerational effects to climate change-related environmental variables and relative environmental change (% of total seasonal variation) applied. The transgenerational response is reported as the change in offspring performance in the altered parental environment compared to offspring from control condition parents (i.e. with the expectation that a positive response reflects adaptive TGP in relation to climate change). If not possible, the comparison has been made against the other appropriate parental treatments

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
Terrestrial invertebrates							
Soil arthropod *Orchesella cincta*	Temperature: heat stress	Adult: only females	Survival eggs / Survival juvenile / Survival adult	Positive / None / Positive	11.4–18.5°C daily variation Liefting and Ellers (2008)	Expected to be outside of normal range	Zizzari and Ellers (2014)
Butterfly *Bicyclus anynana*	Temperature	Adult	Egg size / Offspring provisioning	Positive / Positive	11–27°C Brakefield and Reitsma (1991)	Within normal range	Geister, Lorenz, Hoffmann, and Fischer (2009)
Yellow dung fly *Scathophaga stercoraria*	Temperature	Adult	Egg mortality / Pre-adult mortality / Development time / Growth rate	Negative/None / None / None / Negative/None	Not available	Within normal range Blanckenhorn (1997)	Blanckenhorn (2000)
Fruit fly *Drosophila melanogaster*	Temperature	From early development	Knock down temperature (dam) / Knock down temperature (sire) / Body size (dam) / Body size (sire) / Wing size / Melanisation / Performance breadth / Optimal temperature / Maximum velocity	Positive / None / Negative / None / None / None / None / None / None	11–32°C Zrotta et al. (2006)	Within normal range	Crill et al. (1996)
Milkweed bug *Oncopeltus fasciatus*	Temperature	From early development	Development time / Wing-length (size) / Age at first reproduction / Early-life fecundity	Positive / Positive / None / None	Not available	Within normal range	Groeters and Dingle (1988)
Nematode *Caenorhabditis remanei*	Temperature: heat shock	From early development	Heat shock survival	Negative	Not available	Expected to be outside of normal range	Sikkink, Ituarte, Reynolds, Cresko, and Phillips (2014)
Butterfly *Bicyclus anynana*	Temperature	From early development / Adult	Egg size / Egg size	Negative: Smaller / Negative: Smaller	11–27°C	Within normal range Brakefield and Reitsma (1991)	Fischer, Eenhoorn, Bot, Brakefield, and Zwaan (2003)

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
Aquatic invertebrates							
Marine tubeworm *Hydroides diramphus*	Salinity	Adult	Fertilization success	Positive	25–35 PSU within a day	Within normal range	Jensen et al. (2014)
			Larval survival	Positive			
Bryozoan *Bugula neritina*	Temperature	Adult	Dispersal potential	Positive	15–30°C	Within normal range	Burgess and Marshall (2011)
			Successful metamorphosis	Positive			
Marine polychaete *Ophryotrocha labronica*	Temperature	Adult: early oogenesis	Cold tolerance	Negative	12–27.5°C	16%	Massamba-N'Siala et al. (2014)
			Heat tolerance	Negative			
		Adult: late oogenesis	Cold tolerance	Positive			
			Heat tolerance (loss of control)	Positive			
Cauliflower coral *Pocillopora damicornis*	Temperature and CO_2	Adult	Larval size	Negative	19.5–28.9°C Hunter and Evans (1995) 200–500 µatm Jokiel et al. (2008)	Thermal maximum of normal range 129% CO_2	Putnam and Gates (2015)
			Dark respiration	Positive: Reduced			
			Dark respiration: size corrected	Positive: Reduced in matched parental environment			
Sea urchin *Strongylocentrotus droebachiensis*	CO_2	Adult: 4 months	Larval survival	Negative	pH 7.94–8.16 Yakushev and Sørensen (2013)	109%	Dupont et al. (2013)
		Adult: 16 months	Larval survival	Positive			
Sea urchin *Sterechinus neumayeri*	Temperature and CO_2	Adult: 6 months	Hatching success	Negative	−1.89–1.9°C [*] pH 7.95–8.4 Leggea et al. (2016)	Temperature within seasonal range pH 7.70 = 67% 7.53 = 116%	Suckling et al. (2015)
			Larval survival	Negative			
		Adult: 17 months	Hatching success	Positive			
			Larval survival	Positive			
Sea urchin *Psammechinus miliaris*	CO_2	Adult: 28 days	Larval survival	None	pH 7.97–8.30 Dupont, Havenhand, Thorndyke, Peck, and Thorndyke (2008)	85%	Suckling et al. (2014)
			Growth	None			
		Adult: 42 days	Larval survival	None			
			Growth	Positive			
		Adult: 70 days	Larval survival	None			
			Growth	Positive			
Sydney rock oyster *Saccostrea glomerata*	CO_2	Adult	Development rate	Positive	pH 7.53–9.04 Dove and Sammut (2007)	Within normal range	Parker et al. (2012)
			Growth rate	Positive			
			Survival	None			
Sydney rock oyster *Saccostrea glomerata*	CO_2	Adult: Grandparent	pHe	Positive	pH 7.53–9.04 Dove and Sammut (2007)	Within normal range	Parker et al. (2015)
			Metabolic rate	None			

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
		Adult: Grandparent and from early development	Survival: larval	None	Not available	Expected to be within the normal range	Leung et al. (2013)
			Development rate: larval	Positive			
			Abnormality: larvae	Positive (only 856 µatm)			
			Shell length: larvae	Positive			
			Growth: spat	Positive			
			Heart rate: spat	Negative: Increased			
Polychaete *Hydroides elegans*	Hypoxia	Adult	Development rate	Negative	Not available	Expected to be within the normal range	Leung et al. (2013)
Polychaete *Hydroides diramphus*	Hypoxia	Adult	Development rate	None	Not available	Expected to be within the normal range	Leung et al. (2013)
Crustacean *Daphnia magna*	Hypoxia	Early development	Brood size	None	Not available		Walsh, Whittington, and Funkhouser (2014)
			Neonate release time	None			
			Mass (early development)	Negative			
			Respiration	Negative			
Ascidian *Ciona intestinalis*	Salinity	Early development	Metamorphosis %	Positive	Shallow: 13–34 PSU Deep: 26–35 PSU	Within normal range	Renborg, Johannesson, and Havenhand (2014)
Crustacean *Daphnia ambigua*	Temperature	From early development	Age at maturation	Greater	12–25°C *Dormant during winter	Within normal range	Andrewartha and Burggren (2012)
Brine shrimp *Artemia sp.*	Temperature: heat shock	From early development	Heat shock response	Positive	12–28°C	63%	Norouzitallab et al. (2014)
			Survival	Positive			
Polychaete *Hydroides elegans*	CO$_2$	From early development: Maternal	Larval metamorphosis	Negative	pH 7.6–8.3	Within normal range	Lane, Campanati, Dupont, and Thiyagarajan (2015)
			Juvenile survival	None			
			Juvenile growth	Negative			
		From early development: Paternal	Larval metamorphosis	None			
			Juvenile survival	None			
			Juvenile growth	Positive			
Copepod *Calanus finmarchicus*	CO$_2$	From early development	Development rate (2,080 µatm)	Positive	340–430 µatm Bates et al. (2012)	2,080 µatm = 1,834% 3,080 µatm = 2,946%	Pedersen et al. (2014)
			Development rate (3,080 µatm)	None			

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
Copepod *Pseudocalanus acuspes*	CO_2	From early development	Clutch size (1,500 µatm)	Positive	214–937 µatm Atamanchuk et al. (2015)	900 µatm = 124% 1,500 µatm = 207%	Thor and Dupont (2015)
			Clutch size (900 µatm)	None			
			Egg production (1,500 µatm)	Positive			
			Egg production (900 µatm)	None			
			Respiration rate (1,500 µatm)	Positive			
			Respiration rate (900 µatm)	None			
Marine polychaete *Ophryotrocha labronica*	CO_2	From early development: 7 generations	Fecundity	Positive	pH 7.2–8.4 (30 previous generations)	Within normal range	Rodríguez-Romero, Jarrold, Massamba-N'Siala, Spicer, and Calosi (2015)
Marine polychaete *Simplaria* sp.	CO_2	Multiple generations expected Use of natural CO_2 seeps	Survival	None	pH 7.95–8.11 at control site	Laboratory: 100% Field: 369%	Lucey et al. (2016)
			Reproductive output	None			
			Reproductive frequency	Positive			
			Maturation %	None			
			Population growth	None			
			Individual growth	None			
Fish							
Mangrove rivulus fish *Kryptolebias marmoratus*	Temperature	Adult: 5 days	Pectoral rays	None	17–35°C	Within normal range	Swain and Lindsay (1986)
			Vertebrae	None			
			Caudal rays	None			
		Adult: >40 days	Pectoral rays	Negative			
			Vertebrae	Negative			
			Caudal rays	Negative			
Zebrafish *Brachydanio rerio*	Temperature	Adult	Vertebrae	Increased	6.7–41.7°C Lawrence (2007)	Within normal range	Dentry and Lindsey (1978)
Zebrafish *Danio rerio*	Hypoxia	Adult: 1 week	Length (6, 15, 18 days PF)	Positive	Not available	Expected to be within normal range Lawrence (2007)	Ho and Burggren (2010)
			Length (9–12 days PF)	None			
			Hypoxic resistance	Negative			
		Adult: 2 weeks	Length (6, 9, 12 days PF)	None			
			Length (15–18 days PF)	Positive			
			Hypoxic resistance	Positive			
		Adult: 3 weeks	Length (6–15 days PF)	None			
			Length (18 days PF)	Positive			

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
		Adult: 4 weeks	Hypoxic resistance	Positive			
			Length (6–12, 18 days PF)	None			
			Length (15 days PF)	Positive			
			Hypoxic resistance	Positive			
Sheepshead minnow *Cyprinodon variegatus*	Temperature	Adult: 7 days	Growth (24°C)	None	13–30°C NOAA (2014)	24 and 29 within normal range	Salinas and Munch (2012)
			Growth (29°C)	None			
			Growth (34°C)	None		34°C = 24%	
		Adult: 30 days	Growth (24°C)	Positive			
			Growth (29°C)	None			
			Growth (34°C)	Positive			
Mosquitofish *Gambusia holbrooki*	Temperature (Summer)	Adult	Burst velocity	Negative	8–30°C	Within normal range	Seebacher et al. (2014)
			Critical swimming speed	Positive			
			Resting metabolic rate	None			
			Maximum metabolic rate	Negative			
			Aerobic scope	Negative			
Atlantic Silverside *Menidia menidia*	CO_2/pH	Adult	Survival	Positive	pH_{NBS} 7.2–8.3	Within normal range	Murray, Malvezzi, Gobler, and Baumann (2014)
			Growth	Positive			
Cinnamon clownfish *Amphiprion melanopus*	CO_2	Adult	Survival	Positive	275–542 µatm Albright, Langdon, and Anthony (2013)	581 µatm = 57%	Miller et al. (2012)
			Standard length	Positive		1,032 µatm = 225%	
			Weight	Positive			
			Resting metabolic rate	Positive			
Cinnamon clownfish *Amphiprion melanopus*	CO_2	Adult	Mean burst speed	Positive	275–542 µatm Albright et al. (2013)	581 µatm = 57%	Allan, Domenici, McCormick, Watson, and Munday (2013)
			Max burst speed	Positive		1,032 µatm = 225%	
			Burst response distance	Positive			
			Burst response duration	Positive			
			Burst directionality	Positive			
			Proportion of non-responders	Positive			
Spiny chromis *Acanthochromis polyacanthus*	CO_2	Adult	Lateralization	None	275–542 µatm Albright et al. (2013)	656 µatm = 79%	Welch et al. (2014)
			Olfaction	None		912 µatm = 174%	
Threespine stickleback	Temperature	Adult	Body size 30 days (17 and 21°C)	Positive: dam		Within normal range	Shama et al. (2014)

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
Gasterosteus aculeatus			Body size 60 days (17°C)	None	0–21°C Martens and van Beusekom (2008)		Shama and Wegner (2014)
			Body size 60 days (21°C)	Positive: dam			
			Respiration rate F1 adults (21°C)	Positive: dam			
Threespine stickleback Gasterosteus aculeatus	Temperature	From early development: Parental	Egg size and provisioning	Positive: dam	0–21°C Martens and van Beusekom (2008)	Within normal range	
			Body size 30 days	Positive: sire			
			Body size 30 days	Negative: dam			
			Body size 60 days	Negative: dam			
			Body size 90 days	None			
		Adult: grandparent	Egg size	None			
			Clutch size c	None			
			Body size 30 days	Negative 21°C paternal grandsire			
				Positive 21°C			
			Body size 60 days	Negative & positive 21°C			
			Body size 90 days	None			
Threespine stickleback Gasterosteus aculeatus	Temperature	From early development: Parental	Egg size and provisioning	Positive: dam	0–21°C Martens and van Beusekom (2008)	Within normal range	Shama (2015)
			Body size 30 days	None			
			Body size 60 days	None			
			Body size 90 days	Positive: dam			
Threespine stickleback Gasterosteus aculeatus	Temperature	From early development: Parental	Mitochondrial respiration: OXPHOS	Negative: dam	0–21°C Martens and van Beusekom (2008)	Within normal range	Shama et al. (2016)
			ETS	Negative: dam			
			LEAK	Negative: dam			
		Adult: grandparent	Mitochondrial respiration: OXPHOS	None			
			ETS	Negative & positive: interaction dam and granddam			
			LEAK	Negative & positive: interaction dam and granddam			
Threespine stickleback Gasterosteus aculeatus	Temperature	Adult	Egg size and provisioning	Positive: dam	0–21°C Martens and van Beusekom (2008)	Within normal range	Shama (2017)
			Body size 30 days	None			
			Body size 60 days	None			

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
Spiny chromis *Acanthochromis polyacanthus*	Temperature	Adult	Body size 90 days	None	22.5–29.5°C	+1.5°C = 21% +3 = 42%	Donelson and Munday (2015)
			Gender (+1.5°C)	None			
			Gender (+3°C)	None			
		From early development	Gender (+1.5°C)	Positive			
			Gender (+3°C)	Positive			
Spiny chromis *Acanthochromis polyacanthus*	Temperature	From early development	Resting metabolic rate (+1.5°C)	Positive	22.5–29.5°C	+1.5°C = 21% +3°C = 42%	Donelson et al. (2012)
			Resting metabolic rate (+3°C)	Positive			
			Maximum metabolic rate (+1.5°C)	Positive c			
			Maximum metabolic rate (+3°C)	Positive c			
			Aerobic scope (+1.5°C)	Positive			
			Aerobic scope (+3°C)	Positive			
Spiny chromis *Acanthochromis polyacanthus*	Temperature * +1.5°C, 3.0°C: results are TGP +1.5°C + WGP +3.0°C	From early development	Reproductive timing (+1.5°C)	None	22.5–29.5°C	+1.5°C = 21% +3°C = 42%	Donelson et al. (2016)
			Reproductive timing (+1.5°C, 3.0°C)	Positive			
			Reproductive timing (+3°C)	Negative, no reproduction			
			Breeding proportion (+1.5°C)	None			
			Breeding proportion (+1.5°C, 3°C)	Positive			
			Breeding proportion (+3°C)	Negative, no reproduction			
			Egg area (+1.5°C)	None			
			Egg area (+1.5°C, 3°C)	None			
			Egg area (+3°C)	Negative, no reproduction			
			Clutch size (+1.5°C)	None			
			Clutch size (+1.5°C, 3°C)	Negative			
			Clutch size (+3°C)	Negative, no reproduction			
			Total number of eggs (+1.5°C)	Positive			

(Continues)

TABLE 1 (Continued)

Species	Environmental variable	Exposure time	Phenotypic traits	Transgenerational response	Environmental variation (seasonal range)	Relative change (% of total seasonal variation)	References
			Total number of eggs (+1.5°C, 3°C)	Positive	Not available	Within normal range	Le Roy et al. (2017)
			Total number of eggs (+3°C)	Negative, no reproduction			
Guppy *Poecilia reticulata*	Temperature	Grandparent from early development	Swimming Ucrit:				
			Speed (bl/s) ♀	Positive			
			Speed (bl/s) ♂	Positive			
			Topt ♀	Negative			
			Topt ♂	Positive			
			Performance breadth ♀	None			
			Performance breadth ♂	None			
			Metabolic traits:				
			Resting metabolic rate ♀	Positive			
			Resting metabolic rate ♂	None			
			Maximum metabolic rate	Negative			
			Aerobic scope	Negative			
Amphibians and reptiles							
Moor frog *Rana arvalis*	Temperature	Adult	Larval period	Reduced	Not available	Within normal range	Richter-boix, Orizaola, and Laurila (2014)
			Mass at metamorphosis	Positive			
			Growth	Positive			
Common lizard *Lacerta vivpara*	Rainfall (increased)	Early development: in utero	Litter size	Negative: Decreased	Not available	Within normal range	Marquis et al. (2008)
			Hatchling size	Positive: Increased			
		Early development: conception	Litter size	None			
			Hatchling size	None			
		Early development: juvenile	Litter size	None			
			Hatchling size	None			
	Temperature	Early development: in utero	Litter size	None			
			Hatchling size	None			
		Early development: conception	Litter size	None			
			Hatchling size	None			
		Early development: juvenile	Litter size	None			
			Hatchling size	None			

TABLE 2 Summary of the direction of transgenerational response observed in studies outlined in detail in Table 1. Direction of transgenerational response is shown overall for all taxa, depending on the ecological division (as in Table 1), and in relation to whether the environmental change applied in the experiment was within or outside the normal seasonal range

Transgenerational response	All taxa (%)	Ecological divisions (%)				Relative environmental change (%)	
		Terrestrial invertebrates	Aquatic invertebrates	Fish	Reptiles and amphibians	Outside	Within
Negative	22	22	21	24	7	16	25
None	37	52	32	33	71	33	40
Positive	41	26	47	44	21	51	36

may also be due to the costs of plasticity varying with ontogeny or the overall costs of maintaining genetic machinery for plasticity throughout development, although maintenance costs have been found to be relatively low when examined (Murren et al., 2015). Investigations into TGP associated with climate change more often involve experience by mature adults to projected future conditions rather than plasticity resulting from environmental conditions experienced during early life stages of the parents or previous generations (Table 1). Most commonly, parental experience has been reported to enhance performance of the offspring, but the timing of parental experience is influential (see Table 1). Both the length and timing of an environmental cue experienced by mature parents can affect the transgenerational response observed in offspring (Table 1). Generally, increasing cue length during reproductive phases results in a stronger transgenerational response (Dupont, Dorey, Stumpp, Melzner, & Thorndyke, 2013; Ho & Burggren, 2012; Salinas & Munch, 2012; Suckling et al., 2015; Swain & Lindsay, 1986). For example, parental exposure for 30 days of adult sheepshead minnow to 24°C and 34°C induced beneficial growth in offspring at the respective parental temperature, but TGP was not observed when parents were only exposed for 7 days (Salinas & Munch, 2012). For other species, timing rather than the length of a cue may be essential for producing adaptive TGP. For the marine polychaete, *Ophryotocha labronica*, mothers only provided greater cold or heat tolerance corresponding to parental conditions when temperatures were experienced during late oogenesis (Massamba-N'Siala, Prevedelli, & Simonini, 2014). If the cold and hot conditions were experienced from early oogenesis, tolerance did not match the parental treatment.

Ontogenetic timing of cue exposure throughout parental development can also influence whether offspring phenotype is affected. In the spiny chromis, TGP of offspring gender was only observed when parents developed in elevated thermal conditions from early life, but not if mature parents experienced warm conditions only during the breeding season (Donelson & Munday, 2015). TGP effects may even be restricted to narrow critical windows during the early life of a parent's development. For the common lizard, rainfall experienced by parents in utero, but not at conception or during their early juvenile development, influenced the size and number of offspring they subsequently produced (Marquis, Massot, & Le Galliard, 2008). As experiments begin to add various exposure timings across generations, the patterns of TGP become even more complex. In threespine stickleback, when mature parents were exposed to either 17°C or 21°C, transgenerational effects resulted in better offspring growth in their mother's reproductive environment (Shama, Strobel, Mark, & Wegner, 2014). However, in the following generation when fish were reared throughout development at either 17°C or 21°C, the same transgenerational benefits of maternal reproductive conditions on offspring growth were not observed (Shama & Wegner, 2014). Instead, F_2 offspring exhibited growth benefits during early life in the corresponding temperature of their maternal grandmother (Shama & Wegner, 2014). This suggests that the mechanism(s) underlying the transfer of environmental information differed in the two generations, potentially due to the timing of cue exposure. Acute exposure of mature adults led to optimised mitochondrial respiration in offspring, whereas developmental exposure did not. These physiological differences were also reflected in differential gene expression (transcriptome) profiles of F_2 offspring and likely underlie the differing TGP effects seen for offspring growth depending on environmental cue timing (Shama et al., 2016).

Some differences in when environmental change induces TGP, and when it does not, may be explained by differences in life histories. Attributes such as reproductive strategy (semelparous or iteroparous), parental care, ontogenetic habitat shifts, dispersive life stages, longevity, age at maturity and development rate could all influence if a parent responds to an environmental cue to produce TGP (Burton & Metcalfe, 2014; Herman et al., 2014). Life history attributes that cause parents and juveniles to occupy different environments (i.e. ontogenetic habitat shifts, dispersive life stages) would likely reduce the usefulness of environmental cues experienced during maturity in determining offspring phenotype (Leimar & McNamara, 2015). Instead, parents may rely on the environment experienced during their own early life to trigger transgenerational effects if it serves as a predictor of their offspring's environment (Burton & Metcalfe, 2014). This potentially explains why adaptive TGP is not always observed in experiments with only adult exposure, or why development from early life may be required to express TGP. The expression of TGP will also be influenced by differences in plastic capacity between phenotypic traits and internal trade-offs (Angilletta, 2009; Crill, Huey, & Gilchrist, 1996; Groeters & Dingle, 1988; Seebacher, Beaman, & Little, 2014). For instance, potential trade-offs were observed when summer mosquitofish parents produced offspring with enhanced critical swimming speed, but poorer aerobic capacity and burst velocity (Seebacher et al., 2014; Table 1). Moreover, all phenotypic traits should not be expected to have the same capacity for TGP, as they are not likely to have the same performance optimum or optimal performance range (Clark, Sandblom, &

Jutfelt, 2013; Du, Yan, & Ji, 2000). Unfortunately, our ability to draw conclusions about the influence of life histories on the expression of TGP is restricted by concentrated investigations of a few model species that are easily maintained in laboratory settings and a limited subset of phenotypic traits within each study. There is a need to broaden our understanding of TGP across a range of traits and taxa with differing life histories.

4 | MAGNITUDE OF ENVIRONMENTAL CHANGE

An important aspect of TGP that is largely overlooked in experimental studies is the magnitude of environmental change applied compared to ambient or average conditions. TGP experiments typically involve one treatment and a control, often utilising environmental conditions that are within the seasonal range experienced by the population (Table 1). At best, climate change experiments include three treatments, "mid" and "end" of century predictions plus a control. A relatively large or rapid environmental change can induce a greater set of phenotypic responses than a small or slower change (Kuijper & Hoyle, 2015; Thor & Dupont, 2015), or alternatively, may restrict or alter the plastic changes by causing a stress response that would otherwise not occur with less extreme environmental changes (Badyaev, 2014; Pedersen et al., 2014; Shama, 2017). Furthermore, with a relatively large environmental change, individuals may not be able to produce complete compensation of a trait with just one or two generations (Donelson & Munday, 2015). These studies suggest that thresholds exist for TGP, which may be influenced by the magnitude of natural environmental variation in the system. For example, the copepod *Calanus finmarchicus* from the Northern Atlantic experiences a relatively small seasonal CO_2 range (Bates et al., 2012). In this species, beneficial TGP occurs at moderate CO_2 levels, but not when large increases in CO_2 are applied (Pedersen et al., 2014). In contrast, in the copepod *Pseudocalanus acuspes*, which experiences a relatively large seasonal range (Atamanchuk et al., 2015), parents produce TGP at high CO_2 levels but not at lower levels (Thor & Dupont, 2015). Organisms that experience a relatively small range of environmental variability may exhibit limitations in producing TGP when the environment changes greatly (Donelson & Munday, 2015; Donelson, Munday, McCormick, & Pitcher, 2012; Pedersen et al., 2014), while species that naturally experience greater variation may require a higher level of environmental change before TGP occurs at all (Thor & Dupont, 2015). Prevalence of environmental thresholds may be underestimated by studies only including two experimental treatment levels (i.e. control and treatment) or utilising environmental conditions that are within the seasonal range experienced by the population (Table 1).

Smaller magnitudes of environmental change per generation may be more relevant in attempting to predict the response of species to future climate change, since the end of century conditions will not be reached within a single generation for most species. More gradual or stepwise change across generations can produce differing phenotypic results compared to a single large change within a generation (Donelson, Wong, Booth, & Munday, 2016). Fish that experienced an end of the century relevant increase of +3°C within the first generation and were maintained at +3°C for another generation ceased to reproduce, while fish that experienced +1.5°C in the first generation and another +1.5°C in the second generation (total +3°C over two generations) exhibited improved reproductive capacity compared to the reproductive ability of fish that experienced +3°C in a single generation (Donelson, McCormick, Booth, & Munday, 2014; Donelson et al., 2016). These differences are at least partially due to selection that occurred within the F_1 generation in fish within the +3°C treatment, where only a few fish made up of a particular genetic lineages reproduced (Donelson et al., 2012). However, when comparing the enhanced reproductive capacity of fish that experienced either the gradual generational increase of +1.5°C per generation (totalling +3°C over two generations) versus their siblings that experienced +1.5°C in the first generation and were maintained at +1.5°C for a second generation, there was evidence of WGP on top of TGP when reproducing at +3°C (Donelson et al., 2016). It is thus essential to consider the risks of incorrectly estimating plastic capacity depending on the magnitude of future simulations both within and between generations.

5 | TGP AND OTHER TYPES OF PLASTICITY

There is a growing trend for climate change research to assign phenotypic change that occurs with mutigenerational exposure to TGP, with an absence of exploration or discussion of other types of plasticity. It is naïve to presume that an individual's capacity to transmit transgenerational effects to its offspring will not be influenced by its own capacity for WGP. First, if an individual can effectively produce the optimal phenotype for a given environment with WGP, then TGP would, in theory, not be required. Conversely, in situations where production of the optimal phenotype is restricted within a generation, due to costs and the time required to sense or make changes, greater capacity for TGP is likely (Auld, Agrawal, & Relyea, 2010; Uller, 2008). Higher levels of trait expression can been seen when parent and offspring environments match due to the high degree of temporal correlation (Galloway & Etterson, 2009; Leimar & McNamara, 2015), whereas some species may only possess critical windows during early life that are open to environmental influence to initiate both WGP and TGP (Burton & Metcalfe, 2014; Herman et al., 2014). Perhaps in these cases, capacity for TGP might be more effectively predicted with an enhanced understanding of WGP (Beaman, White, & Seebacher, 2016).

It is plausible that some apparent examples of TGP could actually be a result of developmental plasticity of offspring during early stages, and should rather be treated as WGP. Or alternatively, the interaction between conditions experienced by current and previous generations was not tested and responses should be considered carry-over effects (i.e. the effect of parental environment on

offspring phenotype, regardless of offspring environment). Separation of offspring developmental conditions during early life from parental conditions can be difficult, due to parents brooding the embryos or providing other care that is essential to survival (e.g. nest tending Donelson et al., 2012; Miller, Watson, Donelson, McCormick, & Munday, 2012). Alternatively, if primordial germ cells or developing embryos experience the parental environment, it is difficult to distinguish a true TGP effect from developmental plasticity without completing experiments over two to three generations (Skinner, 2008; Torda et al., 2017). Even in the best model species used to investigate TGP related to climate change, it is unknown when primordial germ cells begin to form, and consequently when there could be direct effects of parental environmental conditions on progeny. The only studies to date that can be certain the observed phenotypic effect in the current generation is due to exposure of previous generations are those that demonstrate grandparental effects (e.g. Herman, Sultan, Horgan-Kobelski, & Riggs, 2012; Le Roy, Loughland, & Seebacher, 2017; Parker, O'Connor, Raftos, Pörtner, & Ross, 2015; Shama & Wegner, 2014). Such studies are, however, the exception rather than the norm. Of course, whether results are truly TGP may not matter if we are only interested in understanding and quantifying the capacity for species to respond to environmental change across generations.

Without more stringent experimental designs in future research, we are limited in our ability to understand TGP and its potential importance in organism responses to environmental change (Figure 1). Clearly, this is most easily achieved in species with external fertilisation where in vitro crosses can be done. It is currently unknown what the relative contributions of WGP and TGP are in most of the observed multigenerational responses (but see Kielland, Bech, & Einum, 2017; Lucey et al., 2016), but it is clear that they can interact in a variety of ways (Luquet & Tariel, 2016). For example, spiny chromis fish exhibited WGP to +3°C conditions in addition to the TGP produced by their parents experiencing +1.5°C conditions (Donelson et al., 2016). Contrastingly, WGP may "overwrite" the occurrence of TGP in the subsequent generation (Burggren, 2015; Shama & Wegner, 2014). A greater understanding of cue timing could also allow us to tease apart cases of TGP from those of carry-over effects (Engqvist & Reinhold, 2016; Uller et al., 2013). Experimental designs that separate effects of developmental conditions from reproductive conditions can begin to partition broad timing effects, as well as TGP from WGP (Figure 1b). Simultaneous investigation of plasticity types is also critical since the same environmental cue can produce either TGP or WGP depending on the phenotypic trait of interest (Figure 1b–d; Beaty et al., 2016).

The interplay between information from previous and present generations will be crucial to the production of both TGP and WGP to climate change (Leimar & McNamara, 2015). For example, in a situation where there is high environmental predictability or stability across generations, it may be more beneficial to use information from the parental generation (and earlier) than to act on an environmental cue only experienced in the current generation. Furthermore, in this example, a large magnitude of change within the present generation might be necessary to override the use of information from a previous generation. However, when the environment varies between generations, especially when this change is of a relatively large magnitude, the offspring phenotypic response may be driven by environmental mismatch between generations rather than the specific environmental conditions experienced (Engqvist & Reinhold, 2016; Shama et al., 2016). Parental effects, where certain parental conditions alter offspring performance across environmental conditions, could substantially impact the offspring phenotypic response within TGP experiments, with many designs used to date being insufficient in allowing separation of TGP from other parental effects (see Engqvist & Reinhold, 2016 for further details). While important theoretical advances are being made on how organisms integrate information from various sources (grandparents, parents and themselves through ontogeny) (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; English, Pen, Shea, & Uller, 2015; Leimar & McNamara, 2015), empirical tests of assumptions and predictions are generally lacking. Experiments that cross individuals from parental environments with a range of within-generation conditions will enhance our understanding of the interaction between plasticity types and the persistence of TGP in further generations, especially when the environment continues to change.

6 | SEPARATING NON-GENETIC AND GENETIC RESPONSES

A limitation of climate change TGP research to date is a general inability to unequivocally distinguish selection from plasticity in experimental designs. Some of the TGP results discussed in this review are likely to not purely be due to plasticity, but may also be influenced by selection of favourable genotypes (via mortality or fecundity differences). In many cases, this may be an inherent logistic constraint of the study system, whereas, in others, appropriate experimental designs could disentangle these effects (Figure 1). One aspect that limits the majority of TGP experiments conducted to date (in non-clonal species) is that parental genotypes are blocked within treatments, and thus, the same genotypes or diversity of genotypes are not present within all treatment conditions (e.g. Miller et al., 2012; Seebacher et al., 2014; Welch, Watson, Welsh, McCormick, & Munday, 2014). Ideal experimental designs are only possible with clonal organisms (see Kielland et al., 2017) or in sexually reproducing organisms that are fully homozygous (e.g. *Arabidopsis thaliana*). Consequently, some of the observed differences in offspring traits between treatments may possibly be due to which genotypes ended up in each treatment and genotype by environment interactions. Nevertheless, random allocation of parental genotypes to exposure treatments (Figure 1a,c) should lead to a similar scope for selection in each treatment. Moreover, when experimental crosses are made between parents from different environments, and for example, F_1 offspring from split-clutches of the same family perform better in their respective maternal environment only, then effects can be confidently attributed to an environment-specific
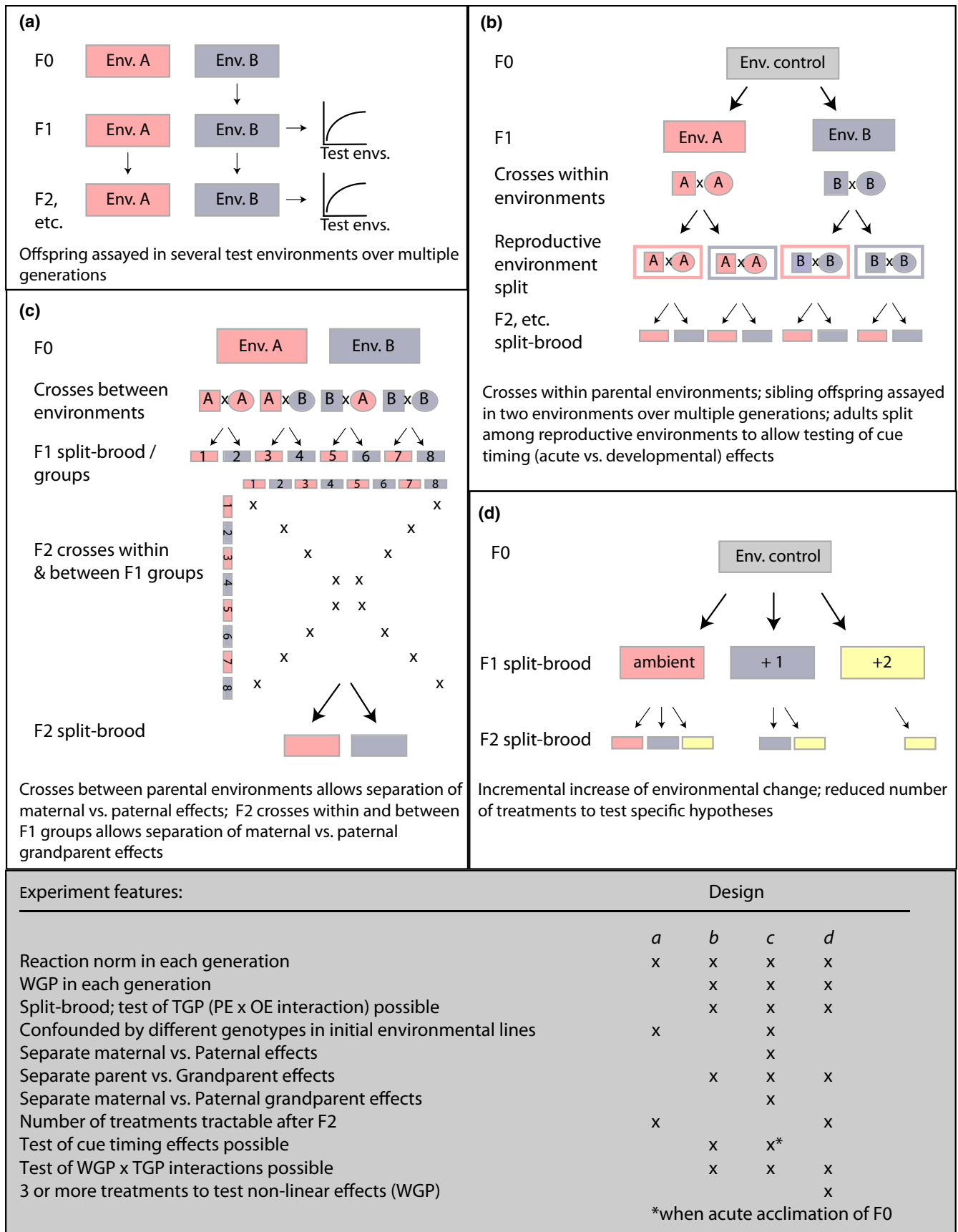
(a)

F0   Env. A   Env. B

F1   Env. A   Env. B → [Test envs.]

F2, etc.   Env. A   Env. B → [Test envs.]

Offspring assayed in several test environments over multiple generations

(b)

F0   Env. control

F1   Env. A   Env. B

Crosses within environments   A x A   B x B

Reproductive environment split   A x A   A x A   B x B   B x B

F2, etc. split-brood

Crosses within parental environments; sibling offspring assayed in two environments over multiple generations; adults split among reproductive environments to allow testing of cue timing (acute vs. developmental) effects

(c)

F0   Env. A   Env. B

Crosses between environments   A x A   A x B   B x A   B x B

F1 split-brood / groups   1 2 3 4 5 6 7 8

F2 crosses within & between F1 groups

```
      1 2 3 4 5 6 7 8
  1   x             x
  2     x         x
  3       x     x
  4         x x
  5         x x
  6       x     x
  7     x         x
  8   x             x
```

F2 split-brood

Crosses between parental environments allows separation of maternal vs. paternal effects; F2 crosses within and between F1 groups allows separation of maternal vs. paternal grandparent effects

(d)

F0   Env. control

F1 split-brood   ambient   + 1   +2

F2 split-brood

Incremental increase of environmental change; reduced number of treatments to test specific hypotheses

Experiment features:	Design			
	a	b	c	d
Reaction norm in each generation	x	x	x	x
WGP in each generation		x	x	x
Split-brood; test of TGP (PE x OE interaction) possible		x	x	x
Confounded by different genotypes in initial environmental lines	x		x	
Separate maternal vs. Paternal effects			x	
Separate parent vs. Grandparent effects		x	x	x
Separate maternal vs. Paternal grandparent effects			x	
Number of treatments tractable after F2	x			x
Test of cue timing effects possible		x	x*	
Test of WGP x TGP interactions possible		x	x	x
3 or more treatments to test non-linear effects (WGP)				x

*when acute acclimation of F0

FIGURE 1 Transgenerational plasticity experimental design approaches. Four commonly used experimental designs (top panels) are displayed to highlight their advantages and limitations (bottom table)

modification transferred from mother to offspring, and not to genetic selection (Shama et al., 2014). However, future experimental designs should include the ability to determine both plasticity and selection independently as well as their interaction, at least in the F_2 generation (Figure 1b–d).

Paramount to disentangling selection from plasticity is the ability to track genetic relatedness (Gienapp et al., 2008). This can be done by genotyping or by maintaining pedigrees, neither of which are commonly done in TGP experiments (but see Donelson et al., 2012; Munday, Donelson, & Domingos, 2016; Shama et al., 2014). TGP experiments require a split-brood design (see Bonduriansky et al., 2012 and Figure 1 for design schematics), and each split-family must be reared individually or marked for later identification. Rearing split-families individually also allows for estimations of WGP, genetic variance for WGP, and their possible interaction with TGP (see above), and can allow for further analyses to disentangle selection from TGP (e.g. fixation index analyses). In clonal species (or homozygotic lineages) distinguishing WGP from TGP is easier and tests of genetic variation for TGP among treatments are possible. For solitary species, experimental designs should start with the same genetic composition of families in all treatments (Vu, Chang, Moriuchi, & Friesen, 2015; Figure 1b,d). Unfortunately, experimental space constraints often limit the number of experimental units (families) and treatments that can be maintained over generations. This is more easily achieved for small organisms with short generation times such as copepods (Thor & Dupont, 2015), other crustaceans (Walsh, Cooley, Biles, & Munch, 2015) and bryozoans (Marshall, 2008), but less so for taxa with longer generation times (Donelson et al., 2012). For larger organisms, it may be that families can be maintained individually only up to a certain size, after which they must be pooled by treatment (see Shama et al., 2014). The problem of disentangling selection from plasticity in multi-generational experiments arises when further generations (F_2 and beyond) are produced from this pool of mixed F_1 individuals. In this case, genotyping parents and offspring in each generation could be used to reconstruct the pedigree (Malvezzi et al., 2015). Additionally, it is essential to track differential mortality and fecundity within experiments to gain an understanding of possible selection. Alternatively, determining whether parental environment effects are reversible can indicate whether plasticity or selection is the driving force. For instance, Jensen, Allen, and Marshall (2014) found that parental salinity environment strongly affected fertilisation success in a marine polychaete. By switching the salinity treatment of half of the adults at the mid-point of the exposure period, they could conclude that plasticity rather than selection was the main driver, as fertilisation success was greatest when the gamete environment matched the parental environment immediately preceding fertilisation i.e. the effects of adult environment were reversible (Jensen et al., 2014).

Separating plastic effects from genetic effects allows studies to address the role of both non-genetic and genetic inheritance in shaping the adaptive potential of populations, but unfortunately is rarely done in the context of TGP studies (but see Hallsson et al., 2012; Kielland et al., 2017; Shama, 2017; Shama et al., 2014). It is important to remember that plasticity itself has a genetic basis and

can evolve (West-Eberhard, 2003), and that both plastic and genetic effects can contribute to a phenotypic trend (Merilä & Hendry, 2014; Munday et al., 2013, 2016; Welch & Munday, 2017). Furthermore, documenting family lines across generations could shed light on the relationship between TGP and the heritability of a trait of interest, as TGP may enhance it, reduce it or have no effect (Bonduriansky & Day, 2009; Munday et al., 2016; Welch & Munday, 2017). One potential avenue of future research is the relationship between evolutionary potential (additive genetic variance *sensu stricto*) and transgenerational effects. Theory predicts that highly plastic traits would be expected to show strong maternal (and/or paternal) effect variance, but little to no genetic variance, because highly plastic traits can be influenced by the environment (also parental environment), and additive genetic variance may be masked by high environmental variation (Lynch & Walsh, 1998). An elegant cross-generational, split-brood study using seed beetles found that a more plastic trait (elytron length) was strongly influenced by parental effects but showed no detectable genetic variance, whereas a less plastic morphological trait showed the opposite pattern (Hallsson et al., 2012), indicating that environment-dependent parental effects may play an important role in the evolutionary response of highly plastic traits. Furthermore, given that the expression of genetic variation can also differ depending on the environment (Hoffmann & Merilä, 1999), it is likely that the relationship between genetic variance and transgenerational effects may be environment-dependent (see Shama et al., 2014). Still, long-term predictions of the effects of non-genetic inheritance on evolutionary potential pose a challenge.

A virtually unexplored aspect of TGP that could be particularly relevant to populations in novel environments (e.g. facing extreme temperatures), is that transgenerational effects could lead to the exposure of cryptic genetic variation. Higher phenotypic variance is commonly seen when individuals are exposed to rare or altogether novel environments within a generation (Ledón-Rettig, Pfennig, Chunco, & Dworkin, 2014; Schlichting, 2008), but can also occur with parental exposure (Shama, 2017). For example, maternal photoperiod of the plant *Arabidopsis thaliana* interacted with offspring temperature, exhibiting varying amounts of phenotypic variation in germination speed depending on the combination (Munir, Dorn, Donohue, & Schmitt, 2001). Similarly, in dandelions, exposing parents to different stresses and raising their offspring in an ambient environment led to an increase of variation in methylation patterns (Verhoeven, Jansen, van Dijk, & Biere, 2010). Additionally, incomplete resetting of epigenetic state can adaptively coevolve with plasticity or maternal effects and prevent mismatch when the environment changes relatively infrequently (Uller, English, & Pen, 2015). Thus, cryptic epigenetic variation and states across generations may also play a role in offering up new phenotypes for selection to act on.

7 | SUMMARY AND FUTURE DIRECTIONS

This review highlights that TGP may be commonplace, but our ability to predict where and when it will be expressed in relation to

projected future climatic conditions is limited. Key to future research is the design of experiments that build on the knowledge to date and admit the limitations that exist, which will depend on the way environmental change is simulated and potential confounding effects in the types of experimental designs used (Figure 1 and Box 1). For many species, we will need to establish a better understanding of how environmental conditions vary over space and time (Burgess & Marshall, 2014) before experimental research can be usefully parameterized. Incorporating relevant magnitudes of environmental change per generation and varying the timing of environmental cues are paramount to acquire the most relevant information for predicting TGP to future global change. As more researchers embark on investigations of TGP climate change, we will inevitably broaden the diversity of species being investigated. This will allow us to understand not only its prevalence, but also the importance of life history and how it may alter the use of environmental cues. Furthermore, including multiple relevant exposure timings in parents will provide essential information on critical time windows that influence the resulting phenotype of offspring. It is our hope that this review helps direct that research in an effective manner.

Theoretical predictions of TGP have advanced faster than experimental tests of these predictions (Walsh et al., 2015), which limits our ability to make robust generalisations, but future research requires a structured approach. Clearly, TGP is not independent of selection or other forms of plasticity. An essential and relatively easy step forward is to separate selection from TGP by tracking identity (genetic and phenotypic) within experiments, and by dividing clones or siblings between treatments (see Bondariansky et al., 2012; Figure 1). Studies that investigate both plasticity and adaptation together allow us to explore the link between evolutionary potential (either additive genetic variation or genotype by environment interactions) and TGP (see Shama et al., 2014; Welch & Munday, 2017). Experimental designs that allow differentiation of WGP from TGP will highlight how these forms of plasticity interact (e.g. overwriting, additive or multiplicative effects), and may allow us to make educated predictions for many species where directly testing TGP is unachievable. Logistically, investigating both WGP and TGP properly will mean experiments with more generations than have often been conducted in the past. This is also important to consider, as more multigenerational experiments are needed to determine how long transgenerational effects persist and if these accumulate or are reset with each generation (Shea, Pen, & Uller, 2011).

Making broad conclusions about the capacity for species to exhibit TGP to projected climate change is made more difficult by the fact that all traits do not show the same capacity for plasticity (Table 1). This may be due to differences in constraints on the rate at which various physiological, morphological or behavioural changes can occur, mechanistic differences in the expression of plasticity, or the environmental thresholds that initiate plasticity of various traits. It is likely that divergent capacity to produce TGP across traits would be common and is underestimated in current research, as studies often investigate a range of closely related traits rather than a diverse array of traits (Table 1). There is a clear need to investigate a

broader suit of performance metrics, ideally incorporating measures of physiology, morphology and behaviour, as well as existing variation in transgenerational effects across individuals in future experiments (Box 1).

The appropriate design of experiments is critical to obtaining accurate predictions of TGP to climate change. Irrelevant exposure timing or cue length for the study species could cause over- or underestimation of TGP potential, especially in the case of adult exposure treatments in longer lived species. Selection of relevant treatment magnitudes is again species- and ecosystem-specific, but we suggest that multiple projected future treatments will assist with predictive capacity. Our ability to comprehend and predict TGP, including the presence of thresholds, the number of generations required for a trait to exhibit full compensation, and the interplay between WGP and TGP, is enhanced by rearing at least two full generations in experiments. Finally, nearly all studies of TGP to date

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BOX 1 Key research areas and considerations for future transgenerational plasticity climate change research

Predictability
- Include relevant environmental variation and estimates of predictability in experimental designs
- Investigate a broader suit of performance metrics: physiology, morphology and behaviour

Cue timing
- Expand research to incorporate environmental cue timing to production of TGP
- Broaden TGP research across a range of taxa
- Consideration of species life history and possible changes across life stages when designing experiments

Magnitude of change
- Consideration of thresholds and relative cue change required for TGP
- Use relevant rates of environmental change within and across generations

TGP and other plasticity types
- Explore variation in transgenerational effects across individuals and the evidence for bet hedging
- Use experimental designs that can distinguish between within-generation and transgenerational plasticity allowing investigation of the interrelationship between plasticity types.
- Incorporation of multiple environmental cues that are projected with climate change

Non-genetic vs genetic responses
- Employ designs that divide siblings or clones between treatments
- Track genetic backgrounds to allow determination of selection vs plasticity

included only one environmental variable (due to the "newness" of investigations for most species), although climate change is expected to alter many critical climatic and biological parameters together. Exploring how TGP shapes traits in response to multiple drivers may help us strengthen our predictions.

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