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Evolutionary rescue via transgenerational plasticity: Evidence and implications for conservation

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Abstract

When a population experiences severe stress from a changing environment, evolution by natural selection can prevent its extinction, a process dubbed "evolutionary rescue." However, evolution may be unable to track the sort of *rapid* environmental change being experienced by many modern-day populations. A potential solution is for organisms to respond to environmental change through phenotypic plasticity, which can buffer populations against change and thereby buy time for evolutionary rescue. In this review, we examine whether this process extends to situations in which the environmentally induced response is passed to offspring. As we describe, theoretical and empirical studies suggest that such "transgenerational plasticity" can increase population persistence. We discuss the implications of this process for conservation biology, outline potential limitations, and describe some applications. Generally, transgenerational plasticity may be effective at buying time for evolutionary rescue to occur.

KEYWORDS
conservation, evolutionary rescue, plastic rescue, transgenerational plasticity

1 | INTRODUCTION

Every natural environment varies, whether in space or in time, and whether owing to biotic or abiotic factors. Moreover, environmental variation can often be experienced by individual organisms, thereby causing mismatches between phenotypes and environments (reviewed in Levins, 1968). Generally, organisms have evolved three main mechanisms to mitigate such costly mismatches (Meyers & Bull, 2002): migrate to a more favorable habitat (e.g., Charmantier & Gienapp, 2014), adapt genetically (Gomulkiewicz & Holt, 1995), or change phenotypes through phenotypic plasticity (the ability of an organism to modify an aspect of its phenotype in direct response to changes in its environment; sensu West-Eberhard, 2003; hereafter, simply "plasticity"). In the face of increasing human-induced

environmental degradation, migrating to more favorable habitats is becoming more difficult (T. B. Smith et al., 2014). Moreover, sessile organisms (e.g., plants, corals) cannot migrate once adulthood is reached. Additionally, in a rapidly changing environment, many species (especially those with longer generation times) may be unable to evolve quickly enough to avoid extinction.

Essentially, for populations faced with rapidly changing environments, the optimal solution may be to respond through plasticity (reviewed in Diamond & Martin, 2016). Although not all plasticity is adaptive (Acasuso-Rivero et al., 2019; Ghalambor et al., 2007), many forms do indeed appear to be associated with an increase in the bearer's fitness (for examples, see Agrawal et al., 1999; Pfennig, 1990; Watt, 1968; Wells & Pigliucci, 2000). Such adaptive plasticity can promote population persistence in novel environments because of its unique

ability to generate a phenotype that matches *current* environmental conditions. A rapid response mediated by plasticity contrasts with evolution, where there is always an intergenerational time lag between when conditions change and when an adaptive phenotypic response can occur.

However, plasticity and genetic evolution are not mutually exclusive. By enabling a population to persist in novel or changing environments, plasticity fosters genetic evolution by "buying time" until genetically based adaptations to accommodate the new conditions can evolve (Fox et al., 2019). For example, once a beneficial environmentally initiated phenotype is produced in a population, selection could continue to promote quantitative genetic changes, leading to a better match between phenotype and environment (West-Eberhard, 2003). Indeed, because plasticity (like most other traits) is often underlain by genetic variation (Kelly et al., 2020), it can undergo adaptive evolution such that a particular plastic response becomes better at matching current conditions. Essentially, plasticity might foster 'evolutionary rescue' (Gomulkiewicz & Holt, 1995), which occurs when adaptive (i.e., genetic) evolution restores positive growth to a declining population, thereby preventing extinction (Carlson et al., 2014). Indeed, elevated levels of plasticity are associated with reduced extinction risk (Ducatez et al., 2020).

Although many researchers appear to acknowledge that plasticity can "buy time" for evolutionary rescue to occur (Fox et al., 2019), it is not clear whether these ideas also apply to *transgenerational* plasticity (sensu Galloway & Etterson, 2007). Transgenerational plasticity occurs when the environment of an individual influences the phenotype of its offspring or later generations (reviewed in Jablonka & Lamb, 1995; Rossiter, 1996). Although it is unknown for how long or how reliably environmentally induced responses can be transmitted in natural populations, even if they persist for only a few generations, they might still increase the chances that a lineage will persist until more permanent genetic changes evolve (Bonduriansky & Day, 2018).

In this article, we review whether and how transgenerational plasticity can buy time for evolutionary rescue. We begin by outlining the role of evolutionary rescue in conservation, along with its limitations. We then evaluate the evidence that transgenerational plasticity can help overcome some of these limitations by allowing populations to persist and serving as the first step toward evolutionary rescue. Finally, we discuss when and how transgenerational plasticity could play a role in conservation biology. By bringing together multiple lines of research on plasticity, nongenetic inheritance, evolutionary rescue, and conservation, we

hope to prompt more research into the field of transgenerational plasticity and its practical applications.

2 | EVOLUTIONARY RESCUE AND ITS CONSERVATION APPLICATIONS

Traditionally, conservation biology has focused on preserving and managing environmental conditions, such as by improving the quality or quantity of suitable habitats. However, recently, conservation biologists have begun to intervene proactively to give populations the ability to survive projected shifts in their environment. Such interventions include: assisted migration (relocating organisms to a more suitable environment, thereby reducing the degree of environment-phenotype mismatch); demographic rescue (captive breeding programs attempting to increase population size); and genetic rescue (introducing conspecifics with a diverse genetic background to augment standing genetic variation; Derry et al., 2019). The aim of these interventions is to accelerate adaptive evolution in a population confronted with a changing or novel environment (van Oppen et al., 2017). Ultimately, the goal is to induce evolutionary rescue.

Essentially, when a population is under severe stress, avoiding extinction is a race between demography and evolution (J. M. Smith, 1989). If environmental change is so abrupt that individuals cannot accommodate the change physiologically or by migrating to more favorable conditions, extinction is a likely outcome (Figure 1a). However, extinction can be avoided if natural selection enriches a population for stress-tolerant genetic variants so that the population regains positive growth rates; that is, if evolutionary rescue occurs (Lindsey et al., 2013). Yet, evolution generally occurs too slowly to prevent an initial decrease in population size with the onset of environmental stress. The classic signature of evolutionary rescue is therefore a U-shaped curve in which population size initially declines in response to environmental stress, and then obtains an adaptive phenotypic change that allows population growth to recover (Figure 1b; Gomulkiewicz & Holt, 1995). The new adaptive phenotype originates either from existing (i.e., standing) genetic variation or through the introduction into the population of new genetic variation via mutation or gene flow/introgression (e.g., see Oziolor et al., 2019). Generally, rescue is more likely to occur in larger populations, which have both more standing genetic variation and a greater supply of individuals in which a beneficial mutation could arise (Bell, 2017).
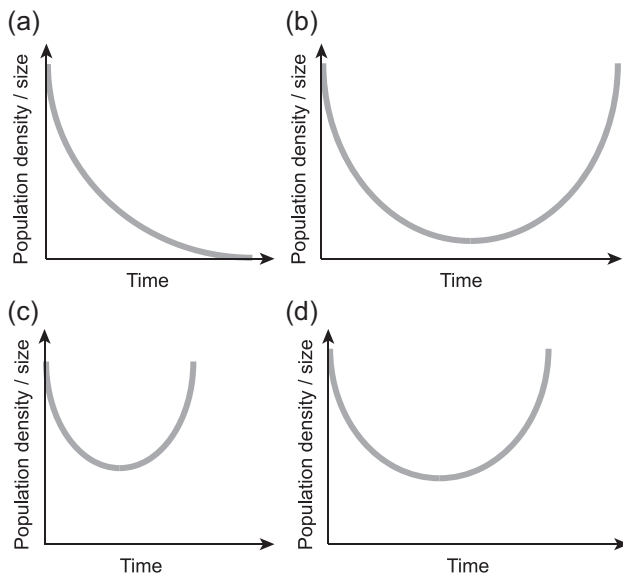
FIGURE 1 Population size across time after abrupt environmental change in a density-independent population unable to migrate. (a) In the absence of adequate plasticity and/or evolution, the population declines to extinction. (b) The population initially declines but may resume growth after adaptive evolution occurs, achieving evolutionary rescue. (c) If plastic rescue precedes evolutionary rescue, the initial maladaptation is immediately lessened, and the rate of adaptation is hastened. (d) Transgenerational plastic rescue preceding evolutionary rescue is intermediate between plastic rescue and evolutionary rescue, as it occurs across a few generations to increase fitness and hasten adaptation

Researchers have long been interested in identifying the mechanisms that allow populations to persist during changing conditions until evolutionary rescue can occur. Models generally show that the likelihood of evolutionary rescue depends on characters of both the population and the environment, such as the size of the population (see above), the supply of genetic variation, and the degree of evolutionary mismatch between the current population mean trait value and the optimum trait value for the experienced environment (Bell, 2017). Other factors can also influence a population's ability to undergo evolutionary rescue, including the mutation rate, the magnitude and nature of environmental heterogeneity, the source and magnitude of gene flow/introgression, and the strength, mode, and direction of selection acting on the population (Bell, 2017). Whether evolutionary rescue is prevalent in nature is unclear, but several laboratory studies have shown that rescue can occur (reviewed in Bell, 2017). One such study exposed hundreds of populations of two species of yeast (*Saccharomyces cerevisiae* and *Saccharomyces paradoxus*) to various concentrations of salt for a hundred generations before transferring them to high salt concentrations that

were lethal to the ancestor (Gonzalez & Bell, 2013). Fitness was greatest for large populations that were adapted to low salt concentrations and for small populations that were adapted to high salt concentrations. In other words, evolutionary rescue was more likely in large populations or where there was a low degree of evolutionary mismatch.

Increasingly, conservation approaches seek to buy time for evolutionary rescue by introducing new individuals or facilitating gene flow among at-risk populations, with the goal of lowering environment-phenotype mismatch and increasing fitness (Vander Wal et al., 2013). However, implementing such strategies can be challenging since many at-risk populations may be depauperate in genetic variation (T. B. Smith et al., 2014) and may therefore lack the ability to evolve quickly enough to keep pace with a rapidly changing environment. Evolutionary rescue therefore remains most likely in organisms with large starting populations and short generation times (McDermott, 2019). However, populations can buy time for evolution by facultatively adjusting their phenotypes within a generation via plasticity. As we explain next, the ability to employ plasticity to produce a new phenotype in oneself and/or offspring that is a better match to the environment could dramatically reduce extinction risk.

3 | PLASTIC RESCUE AS AN INITIAL STEP TOWARD EVOLUTIONARY RESCUE

In the face of environmental change, populations can avoid extinction by exhibiting induced phenotypes that decrease evolutionary mismatch, also known as "plastic rescue." Plastic rescue is generally seen as an immediate––but short-term––method of rescue (Snell-Rood et al., 2018). By allowing populations to adjust to environmental change in "real time" (i.e., in developmental time), plasticity can change evolutionary trajectories and buy time for longer-term evolutionary rescue (Chevin et al., 2013). Here, we describe this process in greater detail. We then suggest that plastic rescue may also lead to evolutionary rescue when plastic responses extend across generations.

3.1 | The buffering role of plasticity

Plasticity serves to buffer the cost of evolutionary mismatch (Ghalambor et al., 2007). Consider an adaptive landscape in which a population resides at an adaptive peak; that is, at its optimum fitness. When environmental

conditions change, the adaptive landscape may also change, which means that the population may no longer reside at a peak. To reach another peak on the adaptive landscape through the standard process of incremental genetic changes, the population must cross a fitness valley, which is normally prevented by selection. With plasticity, however, such valley crossing can occur within an individual's lifetime if plasticity allows it to express a different phenotype closer to an alternative adaptive peak (Pfennig et al., 2010; Price et al., 2003). Plasticity therefore serves as a bridge across adaptive valleys in the adaptive landscape, allowing populations to traverse adaptive valleys and access new adaptive peaks within a single generation. Adaptively plastic phenotypes thus reduce evolutionary mismatch, improving the performance of individuals in response to the environment experienced by themselves or their ancestors (Figure 1c).

Population persistence due to this buffering role of phenotypic plasticity has long been recognized as evolutionarily significant (see Baldwin, 1902; West-Eberhard, 2003). There is much evidence that successful invaders of new habitats and populations undergoing environmental change tend to have high levels of plasticity (e.g., Jablonka & Lamb, 1995; Morris, 2014; Santi et al., 2020). Yet whether plastic rescue is effective when a plastic response can be transmitted *across generations* is less explored.

3.2 | An overview of transgenerational plasticity

As noted above, transgenerational plasticity allows the environment of parents and/or previous generations to shape the phenotypes of offspring through the transmission across generations of environmentally derived stimuli or cues. We use the term transgenerational plasticity to include any nongenetic effects of parental exposure to a particular environmental condition on the offspring, a definition that includes parental effects. With transgenerational plasticity, the parents receive and process environmental cues and then transmit the resulting information to their offspring (Figure 2a–c; A. M. Bell & Hellmann, 2019; Donelan et al., 2020). The offspring must then integrate the information provided by the parent and exhibit an induced phenotype (the offspring may or may not may pass a similar cue to the next generation; Figure 2c; A. M. Bell & Hellmann, 2019). Cues passed between generations could convey a diverse array of information, including epigenetic, nutritional, or cultural information (Bonduriansky & Day, 2018).

There are at least three major categories of transgenerational plasticity (Bonduriansky & Day, 2018). These
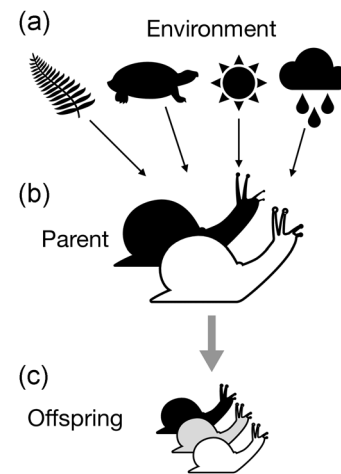
FIGURE 2 Schematic of the flow of information in transgenerational plasticity. (a) Biotic and abiotic factors in the environment provide stimuli or cues (thin black arrows) to an organism, which are (b) processed and may induce a change in phenotype through plasticity (different shading). (c) The processed information may then be used to transmit a cue (gray arrow) to the individual's offspring, which detect and process the information in the cue, which may induce a change in the *offspring's* phenotype through plasticity (different shading). The cue may even be transmitted further to *grand* offspring (not shown)

categories differ in the nature of the mechanism by which the environmentally induced phenotypic response is inherited. The first category involves epigenetic modification. Certain molecules (e.g., methyl groups) can interact with DNA and influence when, where, and how much genes are expressed. Although some such epigenetic factors are determined by DNA sequence, others are induced by environmental triggers, such as diet or stress (Dominguez-Salas et al., 2014). These factors can then be transmitted across generations independently of DNA sequence changes, as when methyl tags are copied onto the daughter DNA strand during DNA replication (Bonduriansky & Day, 2018; Wang et al., 2017). A second main category of transgenerational plasticity involves parental effects. Parents of many species often differentially endow their seeds, eggs, or offspring with acquired information or materials (e.g., cytoplasm, hormones), which can then influence their offspring's phenotype (Mousseau & Fox, 1998). Finally, a third category of transgenerational plasticity occurs through cultural inheritance, prevalent in birds and mammals, which predominately express behavioral plasticity. Cultural inheritance allows individuals to learn a variety of information, such as what and how to eat, what to fear, what mate to attract, and how to attract them (e.g., Aplin et al., 2015; Galef & Laland, 2005). This cultural inheritance allows populations to fine-tune their responses to local conditions and could potentially enable

individuals to take advantage of new resources or change migratory routes within their lifetime (see Jesmer et al., 2018).

Transgenerational plasticity is expected to evolve when: (1) the environment varies or fluctuates predictably beyond one generation; (2) parental environment is a reliable predictor of offspring environment; (3) the cost of plasticity is lower than its benefits; and (4) costs of plasticity are better borne by parents than offspring (Burgess & Marshall, 2014; Dury & Wade, 2020; Kuijper & Hoyle, 2015). Transgenerational plasticity is believed to be taxonomically widespread (Jablonka & Raz, 2009) and occur in response to a wide range of environmental cues (A. M. Bell & Hellmann, 2019). However, with a few exceptions (e.g., see Galloway & Etterson, 2007), the degree to which transgenerational plasticity is *adaptive* remains controversial (Burgess & Marshall, 2014; Sánchez-Tójar et al., 2020; Uller et al., 2013; Yin et al., 2019). Indeed, when considering the prevalence of adaptive transgenerational plasticity, it is important to realize that transgenerational plasticity will likely not be present in every organism or life stage. For example, the timing of environmental cues influences the likelihood that parents can receive, process, and transmit the cue to offspring in an informative manner, and how offspring process cues from parents (A. M. Bell & Hellmann, 2019). It can also be difficult to assess empirically whether transgenerational plasticity is actually adaptive, since a tradeoff might exist between increased fitness early in development and reduced fitness later (Marshall, 2008).

A mismatch between parental and offspring environment can easily yield maladaptive traits (Uller, 2008), but when parents can better assess the environment that offspring will likely encounter than the offspring themselves (e.g., as when parents have better-developed sensory capabilities), transgenerational plasticity can be more beneficial than within-generational plasticity (Burgess & Marshall, 2014; Dyer et al., 2010; Kuijper & Hoyle, 2015). Reliable transmission of environmental information allows for faster and potentially stronger responses to environmental change than within-generational plasticity, as cues are received early in development without the need for offspring to assess their current or future environment (Donelan et al., 2020; Snell-Rood et al., 2015). This early response system may also mean that costs are lower for transgenerational plasticity than plasticity within a generation (Snell-Rood et al., 2018). Transgenerational plasticity may then be especially effective at adaptively modifying offspring phenotype when selective pressures are strong early in life (Donelan et al., 2020). Finally, transgenerational plasticity also can allow for bet hedging, where parents increase the phenotypic variance of offspring, increasing parental geometric mean fitness where environmental conditions are unpredictable (Marshall & Uller, 2007).

Although transgenerational plasticity can allow for the transfer of maladaptive acquired characteristics (as when, e.g., a nutritionally deprived parent produces stunted offspring; Marshall & Uller, 2007), if the offspring environment matches the parental environment, transgenerational plasticity has great potential to be adaptive. An example of adaptive transgenerational plasticity comes from an experiment involving the semelparous herb, *Campanulastrum americium* (Galloway & Etterson, 2007). In this experiment, the maternal generation of plants was raised in either shaded or sunlit environments. Offspring that were grown in the same light environment as their mothers experienced fitness more than three times greater than plants grown in light environments mismatched with their mother. With limited seed dispersal in this system, the maternal environment is a reliable indicator of offspring environment, and offspring indeed experienced greater rates of germination and survival in the environment of their mother (Galloway & Etterson, 2007). Thus, the maternal light environment shaped traits of the offspring in a manner that primed offspring to perform better in their predicted environment.

As we have seen, the buffering ability of plasticity can allow for an immediate adaptive response to environmental change. The further induction of a plastic phenotype across just one generation could therefore make an evolutionary difference, allowing for survival of individuals that could shape future generations. Models show that nongenetic inheritance spanning one to two generations can change the rate and direction of selection, promoting the stability and persistence of a population faster than could be allowed by genetic diversity alone (Geoghegan & Spencer, 2012; Klironomos et al., 2013). Below we review further evidence for this evolutionary role of transgenerational plasticity.

3.3 | Evidence for transgenerational plastic rescue

Despite the similarities of transgenerational plasticity to within generation plasticity, few studies have examined whether transgenerational plasticity (like within generation plasticity) is also capable of acting as a buffer and therefore mediating population persistence. We dub this ability of transgenerational plasticity to promote population persistence "transgenerational plastic rescue" (to distinguish it from "plastic rescue," which refers to within-generation plasticity; Figure 1c). The best

evidence for transgenerational plastic rescue would require comparisons of closely related species or populations that have been exposed to the same environmental stress but that express varying degrees of transgenerational plasticity. If transgenerational plastic rescue occurs, the group with adaptive transgenerational plasticity should persist in a changed environment because of its transgenerational plasticity. In the case of invasive species, we may also expect to see more transgenerational plasticity in successful invaders than in their native competitors.

Most evidence that transgenerational plasticity allows for persistence is indirect, mostly showing that transgenerational plasticity increases fitness (note that it is justifiable to extrapolate that a population possessing traits that increase fitness is more likely to persist; Lande & Shannon, 1996; Schreiber, 2010). There is also a vast and increasing number of studies showing the ability of organisms to quickly adapt to environmental change across generations, but these studies do not often explore the mechanisms of such adaptations, be they transgenerational plasticity or rapid genetic adaptation. That said, there is ample evidence that organisms are able to build stress-resistance across generations via transgenerational plasticity (Table 1; e.g., Morley et al., 2017; Wadgymar et al., 2018). Organisms exposed to stressful conditions across generations generally suffer fitness consequences in the first generation, but then acclimation occurs within relatively few generations (Morley et al., 2017). The effects of such transgenerational plasticity can be on par with those seen in instances of genetic evolution in response to numerous generations of natural selection (Palumbi et al., 2014).

In a study exemplifying transgenerational plastic rescue, marine polychaete worms, *Ophryotrocha labronica*, were reared under conditions of low but variable pH for over 30 generations, over which time they became tolerant of high carbon dioxide partial pressure; that is, pCO_2 (Rodriguez-Romero et al., 2016). When individuals were then raised at either high or low pCO_2, those in the stressful low pCO_2 treatment initially exhibited lower fecundity. By the F3 generation, fitness levels of worms in the low pCO_2 treatment were restored via transgenerational plasticity and maintained at least through generation F7. These F7 individuals also, when transferred, were more fit in the environment matching that of their parents than in the mismatched environment (see also Putnam & Gates, 2015). Fitness was maintained in later generations. However, it was difficult to disentangle the effects of transgenerational plasticity from genetic adaptation. This is therefore potentially not just an example of transgenerational plastic rescue, but of transgenerational plasticity facilitating evolutionary rescue by buffering the population long enough for adaptive genetic changes (i.e., evolution) to occur.

There is also evidence that transgenerational plasticity facilitates invasions (e.g., Dyer et al., 2010; Liebl et al., 2013). Studies of corals and plants found that invasive groups have adaptive transgenerational plasticity or different patterns of DNA methylation that is lacking in non-invasive groups (Fenesi et al., 2014; Hawes et al., 2019). Although it is not yet clear whether transgenerational plasticity often facilitates invasions, or whether it arises because of invasion, the ability to modify gene expression and phenotypes across generations in response to the environment could be key to invasive success. This is because populations with previous exposure to extreme conditions often have increased tolerance of subsequent extremes (Beitinger & Bennett, 2000).

We hasten to add, however, that in some cases transgenerational plasticity may not be adaptive, and rather than contributing to the persistence of populations, it might speed their extirpation (Hughes et al., 2017). Especially when the environment changes rapidly, transgenerational plasticity can be error-prone due to a mismatch of parental and offspring environments and the complex machinery of cue transmission (Donelan et al., 2020). Even when transgenerational plasticity is adaptive, it is rarely known for how long the effects persist and whether the effects persist, accumulate, or even reverse across generations (A. M. Bell & Hellmann, 2019). Thus, literature on the topic is not conclusive as to whether or not transgenerational plasticity tends to be adaptive and promote persistence. The evidence presented here does, however, support the intriguing possibility that transgenerational plasticity can play a role in population persistence. Many studies indicate that plastic responses are beneficial in the new environment, but do not directly show that transgenerational plasticity causes persistence. Moving forward, work ideally will demonstrate that transgenerational plasticity: (1) existed before the environment changed; (2) is adaptive in the new environment; and (3) is responsible for persistence across generations (Morris, 2014).

3.4 | Evidence for transgenerational plastic rescue preceding evolutionary rescue

The goal for conservation is to rescue a threatened population, and perfect plasticity could allow such a population to persist indefinitely in variable environments. Of course, this is unrealistic, and plastic rescue is generally sufficient just for short-term rescue. However, plasticity in a threatened population could promote long

TABLE 1 Diverse ways in which transgenerational plastic rescue could act

Biodiversity threat	Organism	Response
Habitat destruction	Birds	Migratory performance of whooping cranes is learned socially (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013)
	Mammals	New foraging techniques in birds and mammals spread via social learning (Aplin, 2019; Rapaport & Brown, 2008)
		Translocated ungulates learn migratory routes (Jesmer et al., 2018)
Temperature change	Plants	Exposure of Arabidopsis to extreme temperatures results in increased global methylation and greater stress tolerance (Boyko et al., 2010)
	Annelids	Marine polychaetes exposed to temperature stress late in oogenesis have more tolerant offspring (Massamba-N'Siala, Prevedelli, & Simonini, 2014)
	Arthropods	Higher parental temperature reduces caterpillar development times (Steigenga & Fischer, 2007)
	Bryozoa	Offspring of mother bryozoa experiencing warmer temperatures are more likely to successfully metamorphose (Burgess & Marshall, 2011)
	Cnidaria	Corals acclimate transgenerationally (Putnam & Gates, 2015)
	Echinoderms	Sea urchins acclimate transgenerationally to ocean warming (Karelitz et al., 2019)
	Birds	If both parent and offspring zebra finch are exposed to heat stress, hormone priming increases offspring survival (Costantini, Monaghan, & Metcalfe, 2014)
	Fish	Reef fish acclimate to ocean warming transgenerationally (Donelson, Wong, Booth, & Munday, 2016)
	Reptiles	Cultural inheritance of nest-site selection can skew sex-ratios in reptiles with environmental sex determination (Freedberg & Wade, 2001)
Precipitation change	Plants	Offspring of drought-stressed plants survive better in drought (Herman, Sultan, Horgan-Kobelski, & Riggs, 2012)
	Arthropods	Ticks' ability to survive water stress depends upon the humidity experienced by their mother (Yoder, Tank, & Rellinger, 2006)
	Amphibians	The presence of the remains of dead, desiccated spadefoot toad tadpoles induces faster development of future tadpoles (Pfennig & Pfennig, 2020)
	Reptiles	Female live-bearing lizards experiencing more rainfall in utero produce larger hatchlings (Marquis, Massot, & Le Galliard, 2008)
Ocean acidification	Annelids	Marine polychaetes acclimate transgenerationally to ocean acidification (Thibault et al., 2020)
	Arthropods	Transgenerational plasticity mediates fitness decreases in copepods due to ocean acidification (Thor & Dupont, 2015)
	Cnidaria	Corals acclimate transgenerationally to high pCO_2 (Putnam & Gates, 2015)
	Echinoderms	Sea urchins acclimate transgenerationally to ocean acidification (Karelitz et al., 2019)
	Molluscs	Oysters exposed to high pCO_2 during reproductive conditioning have offspring more fit in high pCO_2 (Parker et al., 2012)
	Fish	Clownfish acclimate transgenerationally to high pCO_2 (Miller, Watson, Donelson, McCormick, & Munday, 2012)
Pollution	Arthropods	Cadmium tolerance in amphipods is due to transgenerational plasticity (Vigneron, Geffard, Queau, Francois, & Chaumot, 2019)
	Echinoderms	Maternal exposure to pollutants in urchins enhances offspring tolerance to pollutants via maternal transfer of antioxidant potential (Lister, Lamare, & Burritt, 2017)
	Molluscs	Snails exposed to cadmium have offspring with increased cadmium tolerance (Reategui-Zirena et al., 2017)
	Fish	Maternal exposure to pollutants increases fitness of offspring at the same level of exposure (Nye, Davis, & Miller, 2007)

TABLE 1 (Continued)

Biodiversity threat	Organism	Response
Season shifts	Amphibians	Experimentally delayed breeding in frogs increases offspring growth and development rates (Richter-Boix, Orizaola, & Laurila, 2014)
Overexploitation	Birds	Fearfulness of humans in quail chicks is learned from their mothers (Houdelier et al., 2011)
Disease	Plants	Pathogen attack of plants induces defense phenotypes across generations (Holeski, Jander, & Agrawal, 2012)
	Annelids	Maternal bacterial infection leads to higher antibacterial defense in offspring (Bernier et al., 2019)
	Arthropods	Offspring of immune-challenged brine shrimp have increased resistance to the parental infection (Norouzitallab, Biswas, Baruah, & Bossier, 2015)
	Molluscs	Oyster larvae have higher survival to a virus if their mothers were previously exposed to the virus (Lafont et al., 2019)
	Nematodes	Exposure to pathogens results in transgenerational avoidance of the pathogenic bacteria (Moore, Kaletsky, & Murphy, 2019)
	Birds	Great tit maternal provisioning of yolk androgens in response to parasitism modifies offspring dispersal strategies and increases fitness (Tschirren, Fitze, & Richner, 2007)
	Fish	Discus fish feed larvae a mucus that provides nutrition and protection from infection (Schradin & Anzenberger, 1999)

Note: We list some of the main threats to biodiversity and a sampling of organisms that respond to those environmental impacts via nongenetic mechanisms of inheritance. Within this sample, we include potentially adaptive examples of transgenerational plasticity to illustrate the wide variety of ways in which organisms may experience transgenerational plastic rescue (see Supporting Information for full references).

enough persistence for evolutionary rescue to occur. Plastic rescue is therefore likely a frequent first step toward evolutionary rescue (Morris, 2014).

If parents experience environmental change predictive of their offspring's environment, a population expressing adaptive transgenerational plasticity should be able to track an adaptive phenotype more closely in the face of environmental change than populations lacking such plasticity. Thus, fewer individuals are lost due to maladaptation, and genetic loss is reduced (a frequent goal of conservation efforts). Because the maintenance of genetic diversity reduces the risk of extinction, transgenerational plasticity could therefore buffer a population against extinction by facilitating its persistence. Essentially, transgenerational plastic rescue could result in a larger population with more standing genetic variation and more opportunity for adaptive mutations to arise, thereby facilitating evolutionary rescue (Figure 1d). The presence of stable "epimutations" of small effect (that is, variants caused by errors in epigenetic mechanisms) can allow populations to adapt more quickly than via genetic evolution (Kronholm & Collins, 2016), as well as allow for the preservation of more phenotypic variation (Geoghegan & Spencer, 2012). The signature population curve of transgenerational plastic rescue likely is an intermediate between within-generation plastic rescue and evolutionary rescue, as it occurs on an intermediate timescale (Figure 1b–d).

In addition to facilitating the persistence of populations, an intriguing possibility is that transgenerational plasticity could also promote evolution by exposing genetic variation (i.e., "cryptic" genetic variation) that is normally not translated into phenotypic variation. When this genetic variation is expressed phenotypically and subject to selection, it allows for refinement and potentially canalization of adaptive traits (West-Eberhard, 2003). The decoupling of the phenotype from the genotype permitted by transgenerational plasticity facilitates heritable phenotypic adaptation while reducing genetic loss and allowing for mutations to accumulate (Bonduriansky & Day, 2018). Transgenerational plasticity thus allows for trait distributions to change and for selection to favor these phenotypes and their nongenetic facilitators. The likelihood of getting an adaptive phenotype that can then be genetically canalized is increased (Pal, 1998). However, support for this "plasticity-led evolution" so far centers just on examples of within-generation plasticity (see Levis & Pfennig, 2020).

To support the idea that transgenerational plastic rescue facilitates evolutionary rescue, there should be evidence that persistence due to transgenerational plastic rescue allows for genetic evolution (recall the polychaete example above). Across the time that the population persists, genetic evolution should occur due to the preservation of genetic variation and accumulation of mutations (O'Dea et al., 2016; Snell-Rood et al., 2018). Such

evidence is difficult to document in nature and therefore comes mainly from theoretical studies. In one such study, Klironomos et al. (2013) developed a model of the interplay of heritable epigenetic variants with genetic variants. They showed that with epigenetic variation, populations adapt more quickly and adaptive phenotypic changes appear before any changes in genetics. The adaptive phenotypic changes allow the population size to be maintained (i.e., transgenerational plastic rescue occurs). While a trait is epigenetically (rather than genetically) encoded, mutations can accumulate neutrally. Thus, in mutation-limited populations, the presence of heritable epigenetic variation (i.e., transgenerational plasticity) buffers the population size, allowing adaptation by increasing mutational supply. Similar results have been found by other models (e.g., Geoghegan & Spencer, 2012; Kronholm & Collins, 2016).

Experimental support for transgenerational plastic rescue preceding evolutionary rescue is limited and indirect. For example, two species of stressed yeast, *Saccharomyces cerevisiae* and *S. paradoxus*, were more likely to experience evolutionary rescue if their ancestors had previously been exposed to sublethal doses of the same stressor (Gonzalez & Bell, 2013). Further work on *S. paradoxus* showed that compared to the descendants of unstressed yeast, the descendants of stressed yeast (i.e., salt exposed) were initially more likely to go extinct when encountering the novel salt stress. However, of those that survived, those whose ancestors had been previously exposed to salt were more likely to undergo evolutionary rescue (Samani & Bell, 2016). In other words, rescue of stressed populations enhanced the descendants' ability for evolutionary rescue but decreased their ability to exhibit an adaptive short-term plastic response. However, it is not known whether the prior rescue occurred purely through genetic change or whether it included a plastic response across generations. It is possible that ancestral transgenerational plastic rescue allowed for the accumulation of genetic variation that both rescued the ancestral population and preserved an adaptive evolutionary response in the descendants, but this possibility cannot be determined from the study. Similar studies that evaluate the relationship between plastic rescue and evolutionary rescue will be necessary to understand the extent to which transgenerational plasticity could facilitate or hinder evolutionary rescue.

Other potential evidence for transgenerational plastic rescue preceding evolutionary rescue comes from studies evaluating genetic variation across populations. There is some evidence of genetic variation accumulating in populations that display transgenerational plasticity. For instance, additive genetic variation underlies transgenerational plasticity in antipredator responses of the leaf beetle (*Leptinotarsa decemlineata*; Tigreros et al., 2019). Regardless of whether this genetic accumulation results from the exposure of cryptic genetic variants or from the decoupling of genotypes and phenotypes across generations (as discussed above), such accumulation of genetic variation may allow for canalization of the adaptive plastic responses. If transgenerational plasticity allowed for this accumulation of genetic variation, this would support the idea that transgenerational plastic rescue could facilitate evolutionary rescue.

Finally, it should be noted that transgenerational plasticity may not always, or even often, contribute to evolution. Plasticity can slow or prevent evolution by shielding genotypes from selection (Huey et al., 2003; Mayr, 1963; Wright, 1931). When transgenerational plasticity can increase the duration of time that a population can persist, it remains unknown whether this added time will be enough time to keep pace with environmental change (Fox et al., 2019) and, ultimately, to allow for evolutionary rescue. More research is needed to understand the mechanisms of transgenerational plasticity and its interplay with genetics. Transgenerational plasticity is not an all-encompassing fix for environmental stress, but there is evidence that it could––under the right circumstances––foster persistence and increase evolutionary potential of populations experiencing environmental change. It should also be noted that transgenerational plasticity can buy time not just for a population to undergo evolutionary rescue, but also for the environment to become favorable again or for the population to migrate. Such alternative outcomes of transgenerational plastic rescue also have important conservation implications.

4 | APPLYING TRANSGENERATIONAL PLASTIC RESCUE TO CONSERVATION BIOLOGY

If an aim for conserving populations is to foster evolutionary rescue, transgenerational plasticity (as we have just seen) may be capable of facilitating such rescue. Transgenerational plastic rescue is not a panacea for all threatened species or populations, but there are predictable conditions under which its application is most promising. Organismal characteristics such as motility, social structure, and when the germline departs from the soma, influence the likelihood that they will express various forms of nongenetic inheritance, all of which could constitute transgenerational plasticity (Table 2; Coussi-Korbel & Fragaszy, 1995; Jablonka & Lamb, 1995; van Oppen et al., 2015). Potentially adaptive transgenerational plasticity is expressed in a great

Response type	Factors favoring this response	Example organisms	References
Epigenetic inheritance	Sessile Clonal No or late barrier between soma and germline Low genetic variation	Plants Fungi Bryozoa Cnidaria Echinoderms Molluscs Porifera	Jablonka and Lamb (1995); Liebl et al. (2013); van Oppen et al. (2015)
Parental effect	Fluctuating environment predicted by parent environment Abrupt environmental change	Widespread	Kuijper and Hoyle (2015)
Cultural inheritance	Group living Parental care	Birds Fish Insects Mammals	Aplin et al. (2015); Bonduriansky and Day (2018); Coussi-Korbel and Fragaszy (1995); Jesmer et al. (2018)
Evolutionary Rescue	Large population High genetic variation Short generation time	Plants Insects Rodents Lagomorphs	G. Bell (2017); McDermott (2019)

TABLE 2 Organisms and conditions that may be likely to exhibit transgenerational plastic rescue and/or evolutionary rescue

Note: We list different categories of responses organisms may display in response to environmental change, along with characteristics of organisms or environmental conditions that may predispose them to that response. Some examples of organisms known to exhibit these responses are also included.

variety of organisms in response to environmental change and stressors that pose a threat to biodiversity (Table 1). Thus, the role of transgenerational plasticity in conservation biology should be considered. We describe some potential approaches below, with discussion of their limitations and future directions in the following sections.

A better understanding of transgenerational plasticity (and its underlying mechanisms) is necessary to predict how populations will respond to environmental change (see Donelson et al., 2018). Studies of transgenerational plasticity further emphasize that conditions of rapid and unpredictable environmental change will hinder the ability of populations to respond adaptively through transgenerational plasticity (see Donelan et al., 2020). Thus, the extent to which conservation approaches and policy can act to mitigate or slow the effects of climate change may have a significant ability to conserve threatened populations. However, transgenerational plasticity can also be harnessed to speed evolutionary processes. Such an approach would entail exposing family lines to relevant environmental stressors across multiple generations to induce transgenerational plasticity. If the plastic phenotype in offspring is adaptive across generations, then one could create strains in which transgenerational plasticity can help individuals acclimate to the

environmental stress. Selective breeding of these adaptively plastic individuals could speed the process, allowing one to transplant the tolerant strain into the wild within a few generations. Note that although selective breeding may initially reduce genetic variation, by allowing the population to avoid extirpation, more genetic variation could arise in the long-term as mutation and recombination occur across generations. The approach can also encourage within-generation plasticity and jump-start evolutionary processes, potentially inducing selection for genetic mutations in addition to epimutations (O'Dea et al., 2016).

Although evolutionary rescue is often difficult to achieve in populations with low evolutionary potential (e.g., populations with low levels of genetic diversity), these populations might be good targets for conservation approaches using transgenerational plasticity (Table 2). There is often a negative relationship between the amount of epigenetic diversity and the amount of genetic diversity in a population (Liebl et al., 2013). Therefore, increased diversity of gene expression and epigenetics can compensate for a loss of genetic diversity via the production of adaptive phenotypic variation (Liu et al., 2019). If this pattern holds, small, inbred populations (which are likely to be at risk from human-induced

environmental change) may be particularly suited for the induction of transgenerational plasticity. In these at-risk populations, the interplay of transgenerational plastic rescue and evolutionary rescue should be considered as a conservation tool.

We encourage more research and application of transgenerational plasticity in conservation programs. One promising system to apply transgenerational plasticity to conservation efforts are corals. Coral reefs are under stress around the world, partly because corals (along with their symbiotic algae) are susceptible to sea temperature rise and pH changes from ocean acidification, both of which are associated with greenhouse gas emissions (Hoegh-Guldberg, 1999). Preliminary studies that exposed coral larvae to conditions expected with ongoing climate change (increased temperatures and ocean acidification) found that the coral exhibited the typical signs of transgenerational plasticity: namely, these stressors lowered parental fitness but primed offspring to succeed under the same environmental conditions (Putnam & Gates, 2015). Others have found that even exposure of corals to beneficial conditions improves the fitness and ability of later generations to survive subsequent stress (Rinkevich, 2019). However, not all species or strains will exhibit adaptive responses to transgenerational conditioning (and even after multiple generations of exposure, the trait could return to baseline once the stressor is removed; e.g., Chakravarti & van Oppen, 2018; Sentis et al., 2018). It is also unclear if these acclimatized strains could be transplanted successfully into nature and contribute to successful future generations. Nevertheless, when adaptive, transgenerational plasticity allows for faster phenotypic change in the coral than possible via genetic adaptation (Rinkevich, 2019). Therefore, human assistance inducing transgenerational plasticity allows for lesser maladaptation and increased survival in the face of rapid environmental change. Selectively breeding stress-tolerant strains of coral in the lab is an important first step in being able to transplant these persistent strains in the wild.

As these studies proceed in various coral systems, much remains unknown about the mechanisms of transgenerational plasticity. For example, we need to know how mechanisms of transgenerational plasticity respond to multiple stressors and how they interact with standing genetic variation and within-generation plasticity. A few studies in coral have investigated links between gene expression and plasticity (e.g., Liew et al., 2018; Palumbi et al., 2014), but many mechanisms remain largely unstudied. Of course, there is a lot of groundwork to be done before transgenerational plastic rescue can be fully applied as a conservation strategy in any system. First, it is necessary to identify the relevant stressors under climate change. This may be difficult, but many organisms exhibit a general stress response (Badyaev, 2005; Hoffmann & Parsons, 1991). Induction of such a response by a known environmental trigger may allow for the production of organisms with enhanced tolerance to many future stresses (van Oppen et al., 2017). Second, the organism of interest should be shown to express an adaptive transgenerational response to this stressor. Third, transgenerational plasticity should be investigated thoroughly in the laboratory to understand the relevant timing of the cues and its impact on offspring fitness, including searching for unknown negative effects later in development. This would be difficult and time intensive, but at a minimum, the conditions under which transgenerational plasticity occurs and consequences for individuals should be understood. Ideally, one would also uncover the mechanisms by which cues are received, processed, and transmitted, as well as how multiple and potentially conflicting cues are integrated. Finally, mesocosm and field studies would be needed to discover if findings from the lab hold in natural conditions, particularly whether fitness effects vary due to natural combinations of stressors and whether transplanted individuals are capable of contributing to the next generation. Field tests with tolerant strains should also be used to determine whether these strains enhance demographic performance in their full ecological context.

Once an adaptive transgenerational plastic response is well understood in the lab and under semi-natural conditions (i.e., mesocosms), steps can be taken to consider its use as a conservational tool. Long-term models for the system should be developed to investigate whether the known transgenerational plasticity could facilitate persistence and evolution in the system. No laboratory experiment can fully replicate the balance of stressors, tradeoffs, and selection that occur in the field, but field studies are often extremely complex with large numbers of uncontrolled and possible confounding variables. Multigenerational studies should therefore be conducted in the lab, mesocosms, and field. Only once this point is reached, should tolerant strains be introduced in the wild with reasonable confidence that they will allow populations to persist.

5 | FACTORS LIMITING THE APPLICATION OF TRANSGENERATIONAL PLASTICITY FOR CONSERVATION

Although harnessing transgenerational plasticity through breeding of highly plastic strains is worth investigation, there are challenges with such an approach. For one

thing, transgenerational plasticity may not be present and/or adaptive in all populations, and may not continue to be adaptive across generations, especially when conditions vary between the lab and field environments. Using transgenerational plastic rescue to foster evolutionary rescue is most realistic for populations in which transgenerational plasticity has been observed, studied, and well-understood across multiple generations. However, as noted earlier, this is true for relatively few organisms. Using transgenerational plastic rescue to foster evolutionary rescue also assumes that the populations of interest exhibit variation in their capacity to express plasticity that can respond to selection and increase across generations. Unfortunately, we lack much empirical evidence for these abilities.

In many cases, plastic responses are even known to weaken, reverse, or return to baseline across generations (A. M. Bell & Hellmann, 2019). The persistence or refinement of an adaptive phenotype across generations is most likely to occur in an environment where multiple generations are exposed to the same cue that gradually changes in a directional manner (A. M. Bell & Hellmann, 2019). Transgenerational plasticity is then less likely to be adaptive in climate change scenarios where the environment fluctuates more rapidly (and plasticity within a generation is more likely to be favored; Kuijper & Hoyle, 2015). If parental environment is no longer predictive of offspring environment, transgenerational plasticity might produce harmful offspring phenotypes (Donelan et al., 2020). Determining the extent to which transgenerational plastic rescue could occur in response to future climate change will therefore require studies aiming to understand environmental variation present in the system of interest and the extent to which it is predictable across generations (Donelson et al., 2018).

There is much documentation of within-generation plastic responses to human-induced rapid environmental change (reviewed in Davidson et al., 2011), but very little on the role of transgenerational plasticity (but see Donelan et al., 2020; Donelson et al., 2018). Models predict that transgenerational plasticity could allow persistence in human-altered environments (Fletcher et al., 2012), yet there is doubt as to whether transgenerational plasticity will be able to keep pace with *rapid* environmental change. Human-induced environmental change is characterized by increased environmental stochasticity (IPCC, 2013), which will reduce the extent to which current environmental conditions can predict future conditions. Under such environmental change, parents may not be able to identify the changes or predict offspring environments. In these cases, potentially adaptive parental information could not be integrated into offspring phenotypes (Donelan et al., 2020). This is

because there is necessarily a time lag between parental experience of a stressor, transmission of cue to offspring, and when offspring will encounter the predicted environment. Especially if the environment changes rapidly and unpredictably, there is an increased likelihood for mismatch between parental information and offspring environment. There is therefore an increased likelihood for transgenerational plasticity to be lost or to be maladaptive, especially considering the multiple steps of information transfer in transgenerational plasticity could make the process particularly error-prone (Figure 2; Donelan et al., 2020). Particularly if the environment degrades in a novel manner or degree, transgenerational plasticity cannot provide a solution. As with genetic evolution, transgenerational plasticity is unlikely to produce an adaptive phenotype in response to a truly novel stimulus (i.e., one to which the organisms have had no ancestral exposure).

6 | FUTURE DIRECTIONS

The infancy of research into transgenerational plastic rescue remains the largest constraint in the application of this tool to conservation biology. Gaining an understanding of the mechanisms of transgenerational plasticity will be crucial for determining how transgenerational plasticity works and the extent to which it plays a role in evolution. However, as described above, preliminary studies in coral are promising and suggest that transgenerational plasticity can indeed be applied as a conservational tool. By inducing transgenerational plasticity in the lab, we can facilitate transgenerational plastic rescue and potentially evolutionary rescue. Future work should consider applying similar techniques to other endangered populations, especially those with known adaptive transgenerational responses (see Table 1). Additional research into transgenerational plasticity and evolutionary rescue (Table 3) will increase our knowledge of how transgenerational plastic rescue can play a role in conservation.

More research is needed to clarify the extent and limitations of transgenerational plasticity. In Table 3, we list some areas of research and considerations needed to better understand and apply transgenerational plasticity to conservation biology. As outlined in the previous section, any individual system for which this tool is considered will need to be studied thoroughly to understand the extent and adaptiveness of plastic responses. An increased ability to predict the stressors and degree of environmental degradation that populations will face will also enhance our ability to prepare tolerant strains. Under the right conditions, and perhaps with human intervention, transgenerational plasticity can be the first

TABLE 3 Future directions

- Identify the proximate mechanisms of transgenerational plasticity
- Perform multigenerational studies of transgenerational plasticity
- Study transgenerational plasticity in nature and/or with multiple environmental cues
- Test diverse phyla for adaptive or maladaptive transgenerational plasticity in the context of environmental conditions relevant to climate change
- Investigate the interactions between genetic variation and epigenetic variation
- Study evolutionary rescue and its causal factors in nature
- Explore the interactions between transgenerational plasticity and invasive success
- Explore whether greater genetic variation for transgenerational plasticity increases the probability of rescue
- Investigate the cumulative effects of climate on transgenerational plasticity, population persistence, and evolutionary rescue
- Investigate the relative importance of standing genetic variation, new mutations, and epigenetic variation for evolutionary rescue
- Investigate how the timing of environmental change impacts the likelihood of transgenerational plastic rescue
- Include climate change projections in restoration efforts, and source migrant stock from populations with genetic variation in plasticity
- Take the predictability of environment into account when designing conservation approaches
- Explore the role of transgenerational plasticity in the design of conservation approaches – consider that the environment experienced by ancestors can alter the responses of individuals to predicted environmental conditions
- Explore other avenues by which knowledge of transgenerational plasticity could inform conservation (e.g. how approaches to mitigate or slow the effects of climate change would impact ability to respond adaptively via transgenerational plasticity)

step toward evolutionary rescue necessary for small, endangered populations to avoid extinction.

7 | CONCLUSIONS

In a rapidly changing world, it is imperative to understand whether and how organisms will persist and adapt. The ability of at-risk populations to migrate, evolve, or persist through within generation plasticity are well explored, as is the possibility that such within generation plasticity can buy time for evolutionary rescue. The role of between-generation (i.e., transgenerational) plasticity in mediating

evolutionary rescue is less well known. As we have seen, there is evidence in the literature that transgenerational plasticity can contribute to population persistence. Moreover, such persistence can facilitate genetic evolution and therefore buy time for evolutionary rescue. Finally, as we have also seen, transgenerational plastic rescue could be a powerful conservation tool, although it remains to be seen if it is strong enough to overcome challenges of human-induced rapid (and increasingly unpredictable) environmental change. More research is needed to clarify how transgenerational plasticity acts in various natural systems and the extent to which it can be harnessed as a conservation tool to help populations persist in rapidly changing environments.

CONFLICT OF INTERESTS
The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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