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Resistance and resilience of genetic and phenotypic diversity to "black swan" flood events: A retrospective analysis with historical samples of guppies

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Abstract

Rare extreme "black swan" disturbances can impact ecosystems in many ways, such as destroying habitats, depleting resources, and causing high mortality. In rivers, for instance, exceptional floods that occur infrequently (e.g., so-called "50-year floods") can strongly impact the abundance of fishes and other aquatic organisms. Beyond such ecological effects, these floods could also impact intraspecific diversity by elevating genetic drift or dispersal and by imposing strong selection, which could then influence the population's ability to recover from disturbance. And yet, natural systems might be resistant (show little change) or resilient (show rapid recovery) even to rare extreme events – perhaps as a result of selection due to past events. We considered these possibilities in two rivers where native guppies experienced two extreme floods – one in 2005 and another in 2016. For each river, we selected four sites and used archived "historical" samples to compare levels of genetic and phenotypic diversity before vs. after floods. Genetic diversity was represented by 33 neutral microsatellite markers, and phenotypic diversity was represented by body length and male melanic (black) colour. We found that genetic diversity and population structure was mostly "resistant" to even these extreme floods; whereas the larger impacts on phenotypic diversity were short-lived, suggesting additional "resilience". We discuss the determinants of these two outcomes for guppies facing floods, and then consider the general implications for the resistance and resilience of intraspecific variation to black swan disturbances.

KEYWORDS
floods, *Poecilia reticulata*, population genetic structure, resilience, resistance

1 | INTRODUCTION

A classic approach in evolutionary biology is the interrogation of spatial patterns of genetic or phenotypic variation. The patterns documented through such surveys are frequently used to infer the role of various evolutionary forces, such as natural selection, sexual selection, gene flow, or drift (Endler, 1986; MacColl, 2011; Schluter,

2000). More recently, increasing effort has been directed toward the inclusion of a temporal dimension into spatial-based inferences – either by examining year-to-year changes (e.gGotanda & Hendry, 2014; Siepielski et al., 2009) or decadal-scale patterns (e.gHendry et al., 2008; Leigh et al., 2019; Millette et al., 2020; Parmesan & Yohe, 2003). This integration has generally revealed that temporal variation can be important, but that it usually does not severely

dampen spatial variation. Yet we contend that a key feature of temporal variation deserves more focused consideration. In particular, work on temporal variation often focuses on rather gradual environmental changes, whereas rare but extreme environmental disturbances might permanently impact previous inferences.

Rare but strong disturbances – sometimes called "black swan events" in analogy with the extreme rarity but striking appearance of such birds – can dramatically influence ecosystems and populations (Anderson et al., 2017; Fey et al., 2015). Examples of black swan events can include natural disasters such as hurricanes, earthquakes, storms, or floods that cause mass mortality or emigration (Ameca y Juárez et al., 2012). Several studies have evaluated the impact of black swan events from an ecological perspective by considering how ecosystems cope with disturbances (Mooney & Godron, 1983) –through either "resistance" or "resilience" (Pimm, 1984). The resistance of a system can be thought of as its tendency to avoid displacement from its original undisturbed state, such as when organismal responses buffer the impact of a disturbance. The resilience of a system is defined as its tendency to return to the original state following an initially strong displacement (Pimm, 1984), such as when large immediate changes in community structure later rebound to near the initial state. Of course, these properties can be highly nonlinear, such as when a system resists change until a "tipping point" of disturbance is reached that causes a rapid shift between alternative states (Dakos et al., 2019). Further, the resilience or resistance of a system might change as black swan events increase in frequency, as has been suggested to be particularly likely in the context of climate change (Manyena, 2006).

Most of the existing work on resistance or resilience to black swan events has been ecological in emphasis; that is, it focuses on how natural disturbances influence populations, communities, or ecosystems (Matthews et al., 2014; Reusch et al., 2005). For example, a number of studies quantify the magnitude of mortality in groups of species, and how those species then later recolonize or repopulate the environment and thus re-assemble into "normal" communities (Meffe, 1984; Minckley & Meffre, 1987). In contrast to such studies of interspecific diversity, we have little understanding of how intra-specific diversity is impacted and recovers from natural disasters (Banks et al., 2013). In particular, rare extreme disturbances could have dramatic effects on phenotypic and genetic diversity through changes in natural selection, gene flow, or genetic drift. Some recent examples include contemporary evolution in response to hurricanes (Donihue et al., 2018) and extreme cold or hot weather (Campbell-Staton et al., 2017). Another particularly likely effect of natural disasters on intraspecific diversity is expected to be seen in the meta-population genetic structure of some widely distributed species.

Meta-population genetic structure strongly reflects long term processes that consistently structure the movement of organisms and gametes across the landscape (Orsini et al., 2008). For instance, genetic differences tend to increase with increasing geographical distance (Crispo & Hendry, 2005; Wright, 1943) and as a result of physical barriers to movement, such as mountain ranges, rivers,

waterfalls, or areas of unsuitable habitat (Crispo et al., 2006; Gascon et al., 2000; McRae et al., 2005). However, extreme conditions can occasionally bridge these barriers, creating rafts of vegetation (Waters & Craw, 2018) or nonbiodegradable objects (Carlton et al., 2017). The resulting sudden – even if only temporary – increases of gene flow could disrupt the stability of population structure and have long term effects on neutral or adaptive genetic and phenotypic variation.

The specific context for which we will examine the effects of extreme events on meta-population structure is the occurrence of relatively rare intense floods on fish populations in rivers. Floods generate very high flows that greatly disturb the system state by displacing organisms from their current positions, changing the physical arrangement of the riverbed, carrying mud and debris, and causing high mortality (Resh et al., 1988). Of course, rivers are naturally dynamic systems that experience regular high-flow periods (Lake, 2000; Resh et al., 1988), including in tropical rivers where annual rainfall can be >700 mm/year (Latrubesse et al., 2005). As a result, many organisms in systems subject to periodic high floods show particular adaptations to flood regimes (Lytle & Poff, 2004). Yet some floods are truly exceptional – becoming major black-swan disturbances whose frequency and intensity deviate far from the normal. Examples include sudden flash floods that happen during a dry season (Weese et al., 2011) or exceptionally strong 100-year spring freshets in temperate systems (Matthews et al., 2014). Our study considers how such black swan temporal disturbances might influence typical spatial patterns that reflect longer-term processes.

The spatial meta-population structure of guppies (*Poecilia reticulata*) in the Northern Range mountains of Trinidad is strongly dictated by geographical distance and by waterfalls (Alexander et al., 2006; Barson et al., 2009; Carvalho et al., 1991; Crispo et al., 2006; Fajen & Breden, 1992; Shaw et al., 1994; Willing et al., 2010). For instance, genetic diversity is lower in upstream areas, especially when upstream populations are separated from downstream populations by waterfalls. Similarly, genetic differences between guppy populations are greater when they are separated by greater distances and by waterfalls. In short, guppy population structure is strongly determined by abiotic physical features that limit gene flow in the upstream direction. At the same time, gene flow in the downstream direction is limited by biotic factors, especially the general tendency of guppies to show positive rheotaxis, where they orient and swim upstream in a current (Blondel et al., 2020; Blondel et al., 2020; Mohammed et al., 2012). Yet this biotic resistance to the effects of water flow are sensitive to rare perturbations, such as stream capture events and human-mediated introductions (Becher & Magurran, 2000; Blondel et al., 2019). Another such perturbation could be extreme floods, which are rare but potentially catastrophic.

Guppies in the Northern Range mountains experience regular moderate flooding events during the wet season (Magurran, 2005). The system is clearly resistant to these normal events given the universal documentation of genetic differences associated with distance and waterfalls (Barson et al., 2009; Crispo et al., 2006; Shaw et al., 1994) – but is the system also resistant – or resilient – to the

much larger floods that occur at rare intervals? Over our continuous 20 years of work in Trinidad, our study sites have experienced two extreme floods that had devastating effects on stream ecosystems. Owing to the very local nature of the downpours that cause such floods, they are not always evident on national-level meteorological or hydrological records – but rather are recorded in local newspaper accounts. As an example, in December 2016, the *Trinidadian Guardian Newspaper* reported "torrential rains" that destroyed houses and caused several landslides. At the same time, the *Loop T&T* reported rivers having changed their courses and flowing through properties. To these attestations from the media, we can add our own personal records and photographs (Figures S1–S3).

In our study system, we suggest that signatures of resistance would appear as only minor (if any) changes in genetic diversity and phenotypic diversity after major floods, combined with overall stability of meta-population structure from before to after such floods (throughout this manuscript, "diversity" is used generally to imply variation within or among sites – with distinctions between those levels being noted where relevant.) Finding these signatures could be consistent with either (i) the floods having only minor demographic effects (which we can rule out – see below); (ii) the floods having large demographic effects but still not large enough (or selective enough) to have genetic or phenotypic consequences (Banks et al., 2013); or (iii) existing adaptation to this kind of disturbance (Lytle & Poff, 2004). If, by contrast, major floods had notable genetic or phenotypic effects (i.e., low resistance), signatures of resilience would then appear as a rapid return to preflood genetic and phenotypic patterns.

We tested for these signatures of resistance and resilience by studying genetic diversity, phenotypic traits, and population structure in eight guppy populations located in two watersheds – all experiencing intense floods in 2005 and again in 2016. We leveraged spatial variation among these populations to search for the above signatures of resistance and resilience. On the one hand, high resistance to floods would predict the maintenance of typical patterns: that is, low genetic diversity in guppies at isolated sites (i.e., upstream sites and/or above waterfalls) and their strong differentiation from guppies at other sites. On the other hand, low resistance would predict admixture from upstream and isolated populations into downstream populations, which would modify levels and patterns of genetic and phenotypic diversity. In the case of such low resistance, resilience would then predict a return to original genetic and phenotypic diversity levels and patterns after the flood.

## 2 | MATERIALS AND METHODS

2.1 | Sampling

The guppies genotyped were part of a long-term sampling effort that started in 2002, during which guppies were caught in the same sites each year in February or March. The guppies were captured with butterfly nets, transported to our laboratory in Trinidad, euthanized with MS222, photographed (details below), and preserved in 95% ethanol. For this study, we genotyped fish from our archived ("historical") samples preserved in 2004, 2005, 2016, and 2017 from each of eight sites in the Marianne and Paria Rivers on the north slope of the Northern Mountain Range (Figure 1). We chose these specific years so as to bracket the intensity of two extreme floods – one that took place between January and March 2005 (Weese et al., 2011) and one that took place in December 2016 (pictures of before vs. after floods in Supporting Information). Although we did not directly measure population size before vs. after floods, the black swan nature of these two events was clearly evident. For instance, Weese et al. (2011) reported that the 2005 flood reduced population sizes by "several orders of magnitude", and our catch-per-unit-effort (personal observations) decreased dramatically after the 2016 flood. Further, localized floods in other locations have been shown to have substantial effects on guppy demography (Grether et al., 2001). In each of the two rivers, we chose one site located in the upstream reaches of the main stem, one site located in the downstream reaches of the main stem, one site isolated above a waterfall, and one site in a tributary but not above a waterfall (Figure 1).

2.2 | Genotypes

All genotyping was conducted at Dalhousie University. We extracted DNA using a modified glassmilk protocol (Elphinstone et al., 2003) from fin clips of 1,221 ethanol-preserved guppies (see Table S1 for sample sizes). We genotyped 43 microsatellite loci following the procedures described in Zhan et al. (2017). In brief, we performed two PCRs: 43 loci were amplified in a first multiplex PCR and then we added the indexing sequences to the PCR products in a second PCR. Finally, we sequenced pooled microsatellite amplicons with Illumina MiSeq. Genotypes were scored using the software MEGASAT (Zhan et al., 2017).

All statistical analyses were performed in R using the R studio environment (R Core Studio Team, 2016; R Core Team, 2018), unless otherwise specified. We tested for departures from Hardy-Weinberg equilibrium in each site in each year at each locus using the pegas package (Paradis, 2010), with a sequential Bonferroni correction. We did not test for linkage disequilibrium as these particular loci have been specifically developed to be distributed across the guppy genome (NCBI BioProject PRJNA238429). Gene diversities (Nei, 1973) were calculated using the package poppr (Kamvar et al., 2014) for each sampling site in each year. This measure is similar to expected heterozygosity and represents a quantitative estimate of the genetic diversity within a population. We then used the function Hs.test from the package adegenet (Jombart, 2008) to test for differences in gene diversity before vs. after each flood event for each sampling site. For this test, "individuals are randomly permuted between groups to obtain a reference distribution of the test statistics" (Jombart, 2008), and we did so with 999 permutations for each
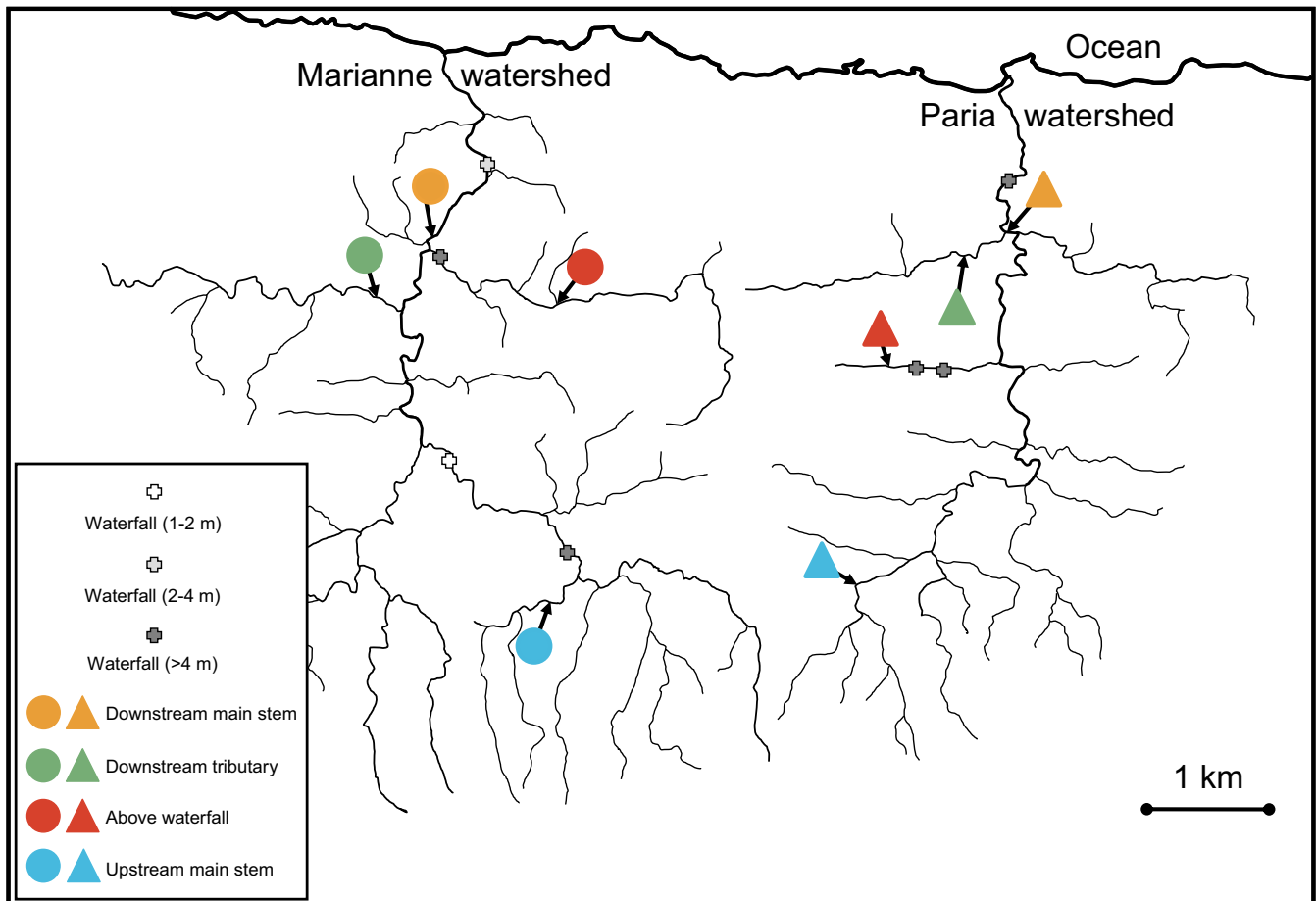
FIGURE 1 Location of sampling sites in the Marianne River (circles) and the Paria River (triangles). In each river, we sampled a site located in the downstream main stem (yellow), a downstream tributary (green), above a waterfall (red), and in the upstream main stem (blue) [Colour figure can be viewed at wileyonlinelibrary.com]

test followed by sequential Bonferroni correction. Allelic richness in each sampling site in each year was calculated using the allelic. richness function in the Hierfstat package (Goudet, 2005). We then built a linear model with allelic richness as the response variable and site (eight levels), flood (two levels: before and after), and their interaction as explanatory variables. All pairwise F_{ST} comparisons were made using the pairwise.ft function in the Hierfstat package (Goudet, 2005). The inbreeding coefficient (F_{IS}) for each individual at each sampling site was calculated using the inbreeding function from the adegenet package (Jombart, 2008). We then built a linear model with F_{IS} as the response variable and the interaction between site and flood as explanatory variables.

We used Bayesian clustering in STRUCTURE (version 2.3.4; Pritchard et al., 2000) to analyse genetic population structure. This method inferred the most probable number of clusters (K) that describe the genotypic distribution. We ran three iterations for each value of K, from 1 to 8 (the total number of sites). Burnin length and run length were each set at 100,000 using the admixture model and the correlated alleles model. We then used the method of Evanno et al. (2005) to find the best K. We extracted the individual admixture data from the STRUCTURE results to compare admixture levels before vs. after the floods. Here, we used a linear model with admixture as

the response variable and site, flood, and their interaction as explanatory variables. A log transformation was used to meet the assumption of homoscedasticity. We carried out post-hoc analysis on the levels of significant terms using the pairwise.t.test function in the stats package, with a Bonferroni correction.

2.3 | Phenotypes

Reflecting improvements made to our methods over the 13 years of sampling, photographs of the fish were taken using different techniques in different years. In 2004, the fish were placed in groups of four or five on neutral-grey graph paper and photographed using a Nikon D100. In 2005, pictures were taken with the same camera or with a Nikon Coolpix 5400 but each fish was placed individually on a white background next to a colour standard. For the 2016 and 2017 pictures, we used the same technique as in 2005 but with a Nikon D800 and D300 respectively.

For all fish in all years, we used the software FIJI (Schindelin et al., 2012) to measure body length as the distance between the anterior end of the mouth and the anterior end of the caudal fin. Due to some missing pictures, these measurements excluded females from

TABLE 1 Measures of Nei's gene diversity (1973) and allelic richness for each sampling site in each year. Significant differences after a sequential Bonferroni correction, before vs. after a flood (2004 vs. 2005 or 2016 vs. 2017) are displayed in bold

River	Category	Gene diversity				Allelic richness			
		2004	2005	2016	2017	2004	2005	2016	2017
Marianne	Downstream main stem	0.51	0.52	0.50	0.53	3.25	3.25	3.09	3.39
	Downstream tributary	0.41	0.43	0.44	0.46	2.87	2.97	2.95	3.08
	Above waterfall	0.39	0.33	0.32	0.32	2.77	2.62	2.45	2.47
	Upstream main stem	0.16	0.17	0.17	0.19	1.56	1.60	1.62	1.70
Paria	Downstream main stem	0.40	0.38	**0.40**	**0.35**	2.76	2.56	2.69	2.39
	Downstream tributary	0.40	0.38	0.37	0.38	2.66	2.56	2.56	2.56
	Above Waterfall	0.22	0.21	0.24	0.24	1.77	1.73	1.78	1.77
	Upstream main stem	0.29	0.29	0.30	0.29	2.13	2.17	2.26	2.16

TABLE 2 Output of the linear models between the several genetic diversity measures and flood, site, as well as their interaction as explanatory variables. Significant terms are displayed in bold

Explanatory variable	df	F	P-value
F_{IS}			
Flood	1	0.08	.774
Site	7	1.75	.094
Site × flood	7	0.60	.757
F_{ST}			
Flood	1	2.23	.138
Pair of sites	55	24.02	**<.001**
Flood × pair of sites	55	1.25	
Allelic richness			
Flood	1	0.05	.829
Site	7	12.12	**<.001**
Site × flood	7	0.27	.967
Genetic Admixture			
Flood	1	1.00	.318
Site	7	50.15	**<.001**
Site × flood	7	6.79	**<.001**

above the waterfall in the Marianne River in 2004, and males from above the waterfall in the Paria River in 2005. We then analysed the variation in body length before and after floods using a general linear model. Body length was set as the response variable, and flood, site and sex were set as explanatory variables, as well as their interaction. A log transformation was used to meet the assumption of homoscedasticity.

To quantify male colour, we used pictures from 2016 and 2017 only, due to lower photograph quality in 2004 and 2005. A colour standard was used to standardize white balance across photographs. For this colour analysis, we used the package patternize (Van Belleghem et al., 2018) to quantify melanic colour patterns for males: we analysed melanic colours only because they were the mostly clearly and unambiguously identified by patternize and because previous work has shown melanic colours vary among our study sites (Millar et al., 2006). Each fish was landmarked in the program FIJI (Schindelin et al., 2012) using nine landmarks. Then, for each site, we selected black colour and analysed it using an RGB threshold. Briefly, the patternize package defines homology between pattern positions across specimens and categorize the distribution of colours using an RGB threshold (Van Belleghem et al., 2018). We then used the pixel coordinates of black colour in a PCA to visualize changes in melanic colour patterns before and after the December 2016 flood. We carried out post-hoc analysis on the levels of significant terms using the pairwise.t.test function in the stats package, with a Bonferroni correction.

3 | RESULTS

Of the 43 microsatellites loci that we genotyped, three were discarded owing to amplification/sequencing errors. We also removed seven loci with 100% missing data in one or more samples. Departures from Hardy-Weinberg equilibrium are visualized as a heatmap (Figure S4) and were randomly distributed among samples and loci – leading to no further exclusions. Thus, the final data set for analysis used 33 loci. Total number of alleles per locus ranged from 3 to 23.

All analyses revealed high resistance of genetic population structure to extreme floods. First, of the 16 before-vs.-after flood comparisons, only one indicated a significant shift in gene diversity. This lone exception was that of the downstream main stem of the Paria River, where gene diversity decreased after the 2016 flood (Table 1, Table 2). Second, no instances did we document a significant before vs. after flood change in pairwise F_{ST} or F_{IS} (Table 2). Not surprisingly
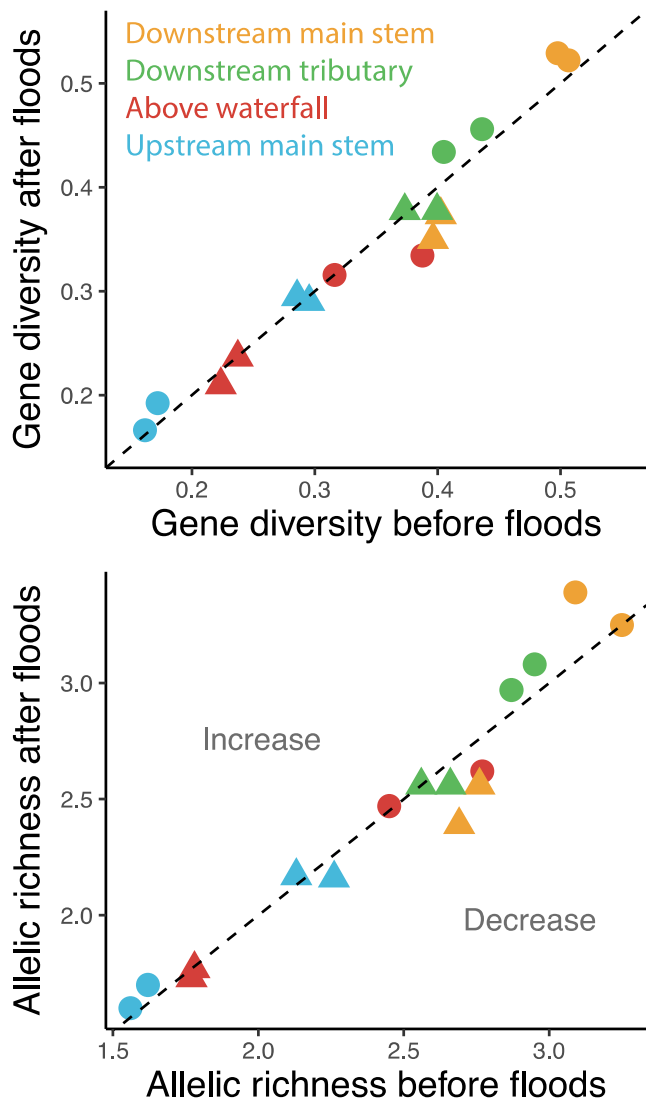
FIGURE 2 Nei's gene diversity (upper panel) and allelic richness (lower panel) before versus after floods for each site category in the Marianne River (circles), and in the Paria River (triangles). Each data point corresponds to either the 2005 flood or the 2016 flood. The one-to-one line represents the case of no change due to a flood. Points above the line represent an increase after a flood and points below the line represent a decrease after a flood [Colour figure can be viewed at wileyonlinelibrary.com]

then, gene diversity differed 3 times more between sites in a given year than between years at a given site (Figure 2, Figure S5). Third, STRUCTURE analysis suggested an optimal number of clusters of $K = 3$ (Figure 3) both before and after floods – with assignment to a given cluster staying the same in all years.

Yet this general resistance to floods does not indicate a complete absence of effects. In particular, STRUCTURE revealed some changes in admixture after the floods at some of the sites (Figure 3). Two noteworthy – and opposing – effects are of particular interest. After the first flood, admixture increased in the site located in the downstream main stem of the Marianne River. Admixture was back to previous levels before the second flood, suggesting the resilience of this population. After the second flood, admixture decreased in the site located in the downstream main stem of the Paria.

In contrast to genetic population structure, analyses of phenotypes showed more obvious immediate effects of floods, as well as some resilience from one flood to the second. In particular, body length systematically increased after floods in the site located upstream in the main stem of the Paria, for both males and females. (Table 3; Figure 4, Figure S6). Overall, size increases after a flood were evident at six of the eight sites for at least one of the sexes for at least one of the events (Figure 4; Figure S6). These increases – at least in the Paria – were tied to decreases in gene diversity (Figure 4). In the seven instances that size increased after the first flood (in the Marianne, males from the downstream main stem, downstream tributary and above waterfalls; in the Paria, males and females from the downstream tributary and downstream main stem; Figure S6), size went back to previous levels before the second flood. In contrast, body length decreased after the 2016 flood for males and females in the downstream main stem of the Paria, and for males in the downstream tributary of the Paria. Male melanic colour patterns also showed some interesting shifts due to floods (Figure 5). In the Paria, for instance, melanic colours decreased after the second flood in the site located downstream in the main stem (Figure S7).

4 | DISCUSSION

Rare catastrophic "black swan" events can cause massive mortality and threaten population persistence (Anderson et al., 2017; Mangel & Tier, 1994). For example, major floods can disturb the physical habitats of rivers (Resh et al., 1988), reduce fish biomass (Grether et al., 2001; Meffe, 1984), and dramatically perturb their population genetic structure (Apodaca et al., 2013; Crispo & Chapman, 2009). For two major local flooding events in Trinidad, we found that the genetic and phenotypic diversity in guppies were mostly resistant, with minimal changes to preflood patterns (Table 1, Table 2; Figure 2, Figure 3). Some upstream-to-downstream dispersal was evident, but its effects were minor (resistance) and temporary (resilience). By contrast, phenotypic diversity was more heavily impacted in the short term but then mostly recovered – thus showing more resilience than resistance to these events (Again, "diversity" is used in a general sense to be inclusive of within and among population variation and patterns.).

4.1 | Resistance

After the two floods, patterns of genetic variation stayed relatively stable (Figure 3). That is, we did not observe major changes in genetic diversity or allelic richness (Table 1) and the increase in gene flow was minimal (Table 2). These results support previous findings in some other fishes that observe little change between pre- and post-flood values of genetic diversity, and minor to no downstream displacement after severe floods (Franssen et al., 2006; Plath et al., 2010; Pujolar et al., 2011). Several hypotheses can explain the strong resistance of these populations to such black swan events.

Marianne

Paria
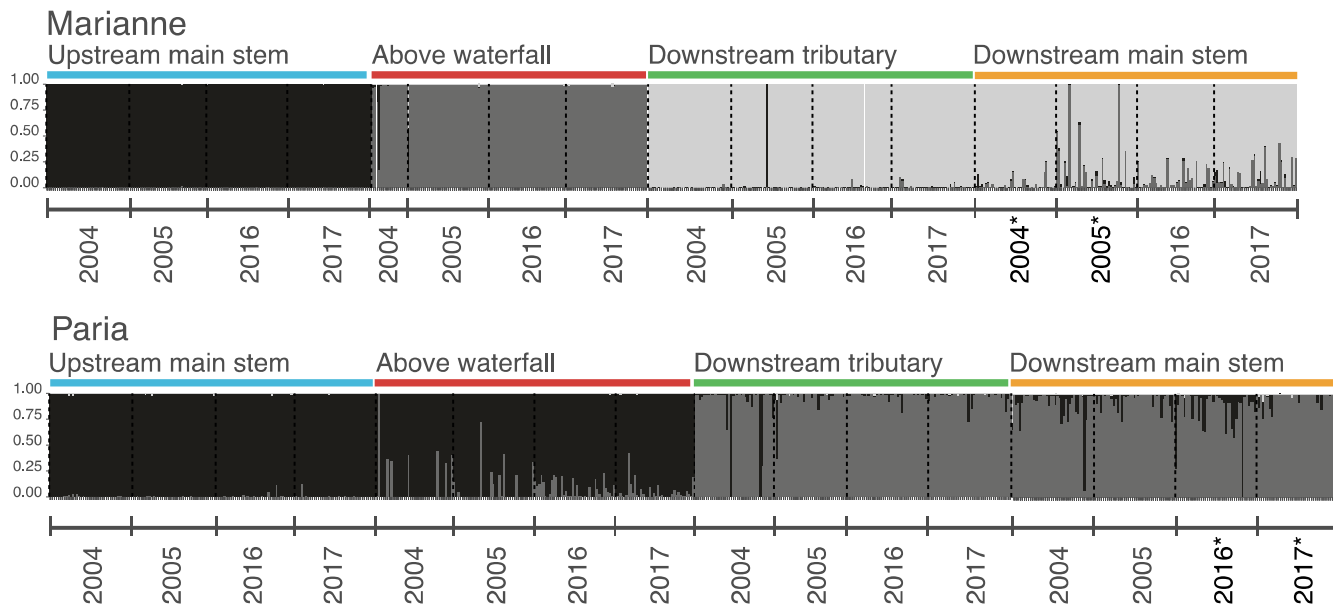
FIGURE 3 Results of the STRUCTURE analysis. Every vertical line represents an individual and is shaded according to its cluster assignment. The optimal number of clusters was $K = 3$. When an individual bar shows multiple shades, it reflects individual admixture among clusters. Significant increases or decreases in admixture between years are indicated by an asterisk following the year [Colour figure can be viewed at wileyonlinelibrary.com]

First, guppies and other stream fishes have evolved adaptations to cope with the effects of periodic high-water velocities. Behavioural mechanisms include hiding, maintaining their position in the stream, or orientating quickly and efficiently against the flow as evidenced in guppies (Blondel, Klemet-N'Guessan, et al., 2020; Blondel, Paterson, et al., 2020) and other fishes (David & Closs, 2002; Meffe, 1984). Adaptations can also be evident in life history traits, where organisms synchronize reproduction events in season with low flow probability (Lytle & Poff, 2004). Although guppies reproduce all year long, Reznick (1989) found that females had fewer offspring during the wet season – the season with the highest probability of floods.

Second, it is possible that high levels of dispersal occurred but had little effect on genetic variation owing to high mortality overall – and especially for migrants. Indeed, strong adaptive divergence between upstream (often low-predation) and downstream (often high-predation) guppy populations (Reznick et al., 2001) suggests that migrants from the former to the latter would have minimal effects on the downstream populations. Indeed, this mechanism is supported by an experimental study of some of the same sites, which focused on the natural and sexual effects of selection against migrants after the first flood (Weese et al., 2011). In particular, in high predation environments, low-predation guppies had lower survival probability than high predation ones, and low predation males sired fewer offspring than high-predation ones.

Third, another potential explanation for the resistance we observed is that the floods were not strong enough – that is, they were more "normal" than at the "black swan" level. It is hard to be definitive in this regard owing to the lack of detailed hydrological monitoring. For example, we could not directly measure water discharge or flow velocity in each site, and the effects appear to

be very localized. Yet, we do not think this is true considering the extent of the two floods that stood out in our 20 years of sampling these sites (Figures S1, S2, S3), and the large demographic effects that we observed. It does remain possible that the demographic effects were large but still not sufficient to have appreciable effects on diversity. For example, genetic effects might only be evident when population sizes get below some extreme threshold (Peakall & Lindenmayer, 2006) and, even then, it might take some time for those effects to be manifest (Leigh et al., 2019; Millette et al., 2020; Stoffel et al., 2018). At the phenotypic level, the lack of observable effects might simply mean that the flood effects were nonselective, although that seems unlikely in

TABLE 3 Output of the linear model for body length and male melanic colours. Significant terms are displayed in bold

Explanatory variable	df	F	P-value
Body length			
Site	7	48.22	**<.001**
Flood	1	0.00	.991
Sex	1	65.66	**<.001**
Site × flood	7	18.84	**<.001**
Site × sex	7	6.50	**<.001**
Flood × sex	1	0.64	.424
Site × flood × sex	7	5.09	**<.001**
Male melanic colour			
Site	7	14.65	**<.001**
Flood	1	0.80	.448
Site × flood	7	6.63	**<.001**
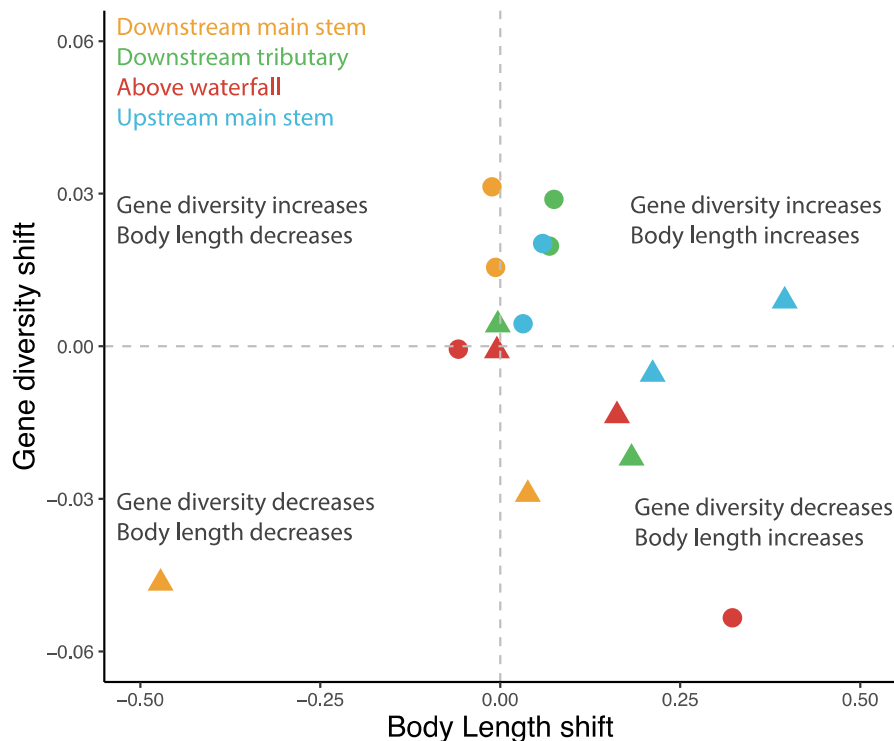
guppies (Fitzpatrick et al., 2014; van Oosterhout et al., 2007) , and for organisms that experience extreme climatic events in general (Coleman & Wernberg, 2020) .

Although we generally observed strong signatures of resistance to floods in most of the guppy populations, one site – located downstream in the main stem of the Paria – was noticeably impacted. In this site, admixture decreased after both flood events (Figure 3). For instance, after the second flood, gene diversity decreased by 12.5% (Table 1), body length for males and females decreased by 25% (Figure 4) and melanic colour patterns shifted towards less melanics (Figure 5, Figure S7). We hypothesize that because this site is located at the junction of the main stem and of two tributaries, it usually (under nonflood conditions) represents a mix of local fish and immigrants from the upstream tributaries. In the case of a catastrophic flood, guppies from all locations are displaced and genetic diversity decreases – hence, contrary to the initially expected scenario, a major flood may have "purged" this site of the immigrants it normally harbours under more benign normal conditions. Major predators are lacking throughout the Paria River and so the above mentioned "selection against immigrants" might be minimal at this site in the absence of a flood.

4.2 | Resilience

Although the guppy system seems mostly resistant to the floods, we could see some signatures of resilience emerging from temporal changes at some of our study sites. First, increased levels of admixture in the downstream main stem site in the Marianne after the first flood went down to preflood levels 11 years later (Figure 3). We

explain this increase after the flood by elevated gene flow to this downstream site, probably receiving migrants from more upstream sites, thereby increasing the genetic signature of fish from another genetic cluster (Figure 3). However, this genetic signature did not last, and admixture went back to preflood levels, which might be explained by selection against upstream migrants into downstream sites (Weese et al., 2011).

Body length showed low resistance to the two floods. In six out of the eight sites, we found that, after floods, body size increased for either males, females or both (Figure 4; Figure S6). This result suggests that floods are selecting against small guppies. Several hypotheses could explain this finding. First, small size guppies could be less efficient at swimming against the flow, and thus more likely to be swept downstream. Second, small size guppies could be more sensitive to the effect of the floods and suffer from higher mortality than bigger guppies. Whenever these changes in body length happened during the first flood, guppy body length was back to preflood size before the second flood suggesting resilience of this phenotypic trait.

4.3 | Resistance vs. resilience

We found that most aspects of guppy population genetic structure were highly resistant to floods. This resistance might be only "apparent," such as if the disturbance was not actually that severe (see above), although this seems unlikely because of the observed dramatic demographic effects (Weese et al., 2011; personal observation). Hence, resistance was more likely due to mechanisms guppies have evolved that resist displacement from their home

FIGURE 5 PCA plots of the male melanic colour pattern for each site in each watershed. Grey squares are individuals from 2016, black points are individuals from 2017. PC axis are unique to each site and represent the coordinates of the black pixels in our photographs [Colour figure can be viewed at wileyonlinelibrary.com]
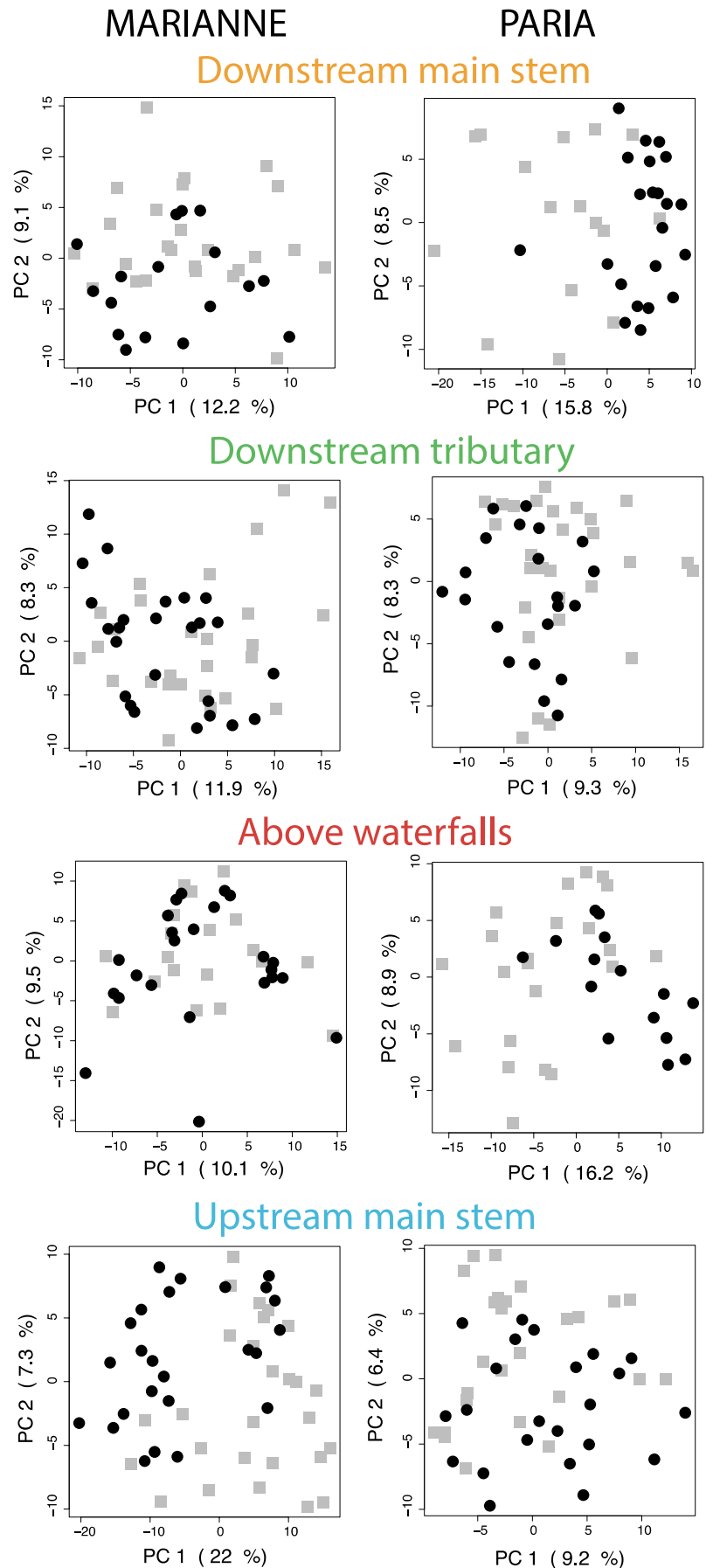
sites, including the avoidance of high current and the evolution of positive rheotaxis (Blondel, Klemet-N'Guessan, et al., 2020; Blondel, Paterson, et al., 2020) . By contrast, phenotypic variation was not as resistant as genetic variation – which might be due to several factors. In particular, the genetic markers we used to infer population structure are neutral loci, which can be subject to a time lag between disturbance and effect (Epps & Keyghobadi, 2015). On the contrary, phenotypic traits are a product of the interaction between genes and the environment and might be more likely to reflect any immediate disturbance, either because of differential selection or phenotypic plasticity (Labonne & Hendry, 2010).

Generally, we suggest that biological systems are likely to converge on either strong resistance with little resilience or vice versa. The reason is that, if a system is highly resistant, then little opportunity exists to manifest resilience: that is, if no change occurs due to disturbance (thus high resistance) then recovery from disturbance (high resilience) is moot. Importantly, this argument applies at the whole-system level. Individuals, by contrast, still could be experience natural selection for traits that promote resilience and, thus, a displaced individual could still manifest behaviours that enhance resilience. In cases where a system is not very resistant (a disturbance causes large genetic or phenotypic change), those individual behaviours that enhance resilience (e.g., return to home site) then could be important in generating resilience – as could ongoing selection after the disturbance. Given this expected "trade-off" at the system level (either resistance or resilience but probably not both), we might ask what sorts of systems will converge on resistance or resilience? One possibility favouring resistance might be constraints (such as waterfalls) that limit the potential for resilience. That is, if a guppy is washed over a waterfall, it cannot very well just swim back. One possibility favouring resistance might be the rapidity of potential recovery response – as argued above for phenotypic traits as opposed to neutral markers. We urge further work on the balance between resistance and resilience of genetic and phenotypic variation in responses to such determinants.

DATA AVAILABILITY STATEMENT

Phenotypic and genotypic data are accessible from Dryad. https://doi.org/10.5061/dryad.wwpzgmsh8 (Blondel, Paterson, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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