Ecological correlates of the distribution limits of two poeciliid species along a salinity gradient

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Identifying the environmental factors responsible for the formation of a species' distribution limit is challenging because organisms interact in complex ways with their environments. However, the use of statistical niche models in combination with the analysis of phenotypic variation along environmental gradients can help to reduce such complexity and identify a subset of candidate factors. In the present study, we used such approaches to describe and identify factors responsible for the parapatric distribution of two closely-related livebearer fish species along a salinity gradient in the lowlands of Trinidad, West Indies. The downstream distribution limits of *Poecilia reticulata* were strongly correlated with the brackish–freshwater interface. We did not observe significant phenotypic variation in life-history traits for this species when comparing marginal with more central populations, suggesting that abrupt changes in conditions at the brackish–freshwater interface limit its distribution. By contrast, *Poecilia picta* was present across a wide range of salinities, although it gradually disappeared from upstream freshwater localities. In addition, *P. picta* populations exhibited an increase in offspring size in localities where they coexist with *P. reticulata*, suggesting a role for interspecific competition. The parapatric distribution of these two species, suggests that *P. reticulata* distributions are limited by an abiotic factor (salinity), whereas *P. picta* is limited by a biotic factor (interspecific competition). Similar parapatric patterns have been previously described in other systems, suggesting they might be a common pattern in nature. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **108**, 790–805.

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INTRODUCTION

The niche of a species is defined by the set of all ecological factors under which intrinsic population growth remains positive (Hutchinson, 1957). The niche concept has played a central role in the development of ecological theory (Chase & Leibold, 2003) and its importance to biogeography has also long been emphasized (Grinnell, 1917), receiving heightened attention in the last decade in the context of species distribution limits (Pulliam, 2000; Soberón, 2007; Angert, 2009; Holt, 2009; Chase & Myers, 2011; Peterson *et al.*, 2011; Wiens, 2011). Theory predicts that mismatches between a species' niche and local habitat should result in negative population growth. If mismatches occur as a result of environmental gradients, one outcome is the formation of distribution limits because the net gain of individuals at a certain point along the gradient no longer exceeds the net loss (Gaston, 2003). Thus, the niche influences processes at local scales, which in turn shape biogeographical patterns at regional scales (Gaston, 2003; Soberón, 2007; Wiens, 2011). Yet, a major challenge in ecological and biogeographical studies is determining which factors that define a species' niche play the most important roles in the formation of distribution

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patterns. Identifying these factors is particularly difficult as a result of complex interactions that can emerge along environmental gradients (Vannote *et al.*, 1980; Attrill & Rundle, 2002), as well as at varying spatial scales (Fausch, Nakano & Ishigaki, 1994; Poff, 1997).

Climatic factors such as temperature and precipitation are often identified as being responsible for the formation of species range limits and large-scale biogeographical patterns (Gaston, 2003; Lomolino, Riddle & Brown, 2006). However, at small geographical scales, evidence suggests that other abiotic factors determine species' distribution limits (Sexton *et al.*, 2009; Wiens, 2011). For example, in aquatic systems, some of the most relevant factors are water salinity, flow, temperature, and dissolved oxygen (Allan & Castillo, 2007). Water salinity is particularly important for both marine and freshwater organisms because ionic balance is crucial for osmoregulation and homeostasis (Nordlie *et al.*, 1991). Therefore, salinity can directly affect components of fitness, such as survival (Shervette, Ibarra & Gelwick, 2007), as well as several traits related to fitness, such as behaviour (Peterson-Curtis, 1997), growth rate (Bœuf & Payan, 2001), and other life-history traits (Gomes & Monteiro, 2007), and has the potential to be an important factor affecting aquatic species distributions (Marshall & Elliott, 1998). Steep gradients in salinity occur where rivers discharge into the sea, forming estuarine environments (Winemiller & Leslie, 1992; Attrill & Rundle, 2002). Yet, the role of salinity as an important abiotic factor in shaping species distributions is more often assumed than tested empirically.

Abiotic factors alone can shape species distribution limits; however, numerous lines of evidence suggest that abiotic factors frequently interact with biotic factors to determine these limits (Sexton *et al.*, 2009; Coulson *et al.*, 2011). For example, competitive dominance among species can switch along abiotic gradients, leading to parapatric distribution limits (Hairston, 1949, 1980; Connell, 1961; Dunson & Travis, 1991; Taniguchi & Nakano, 2000; Martin & Martin, 2001; Twomey, Morales & Summers, 2008). Yet, the importance of interspecific competition and other biotic interactions along abiotic gradients are often overlooked in most niche models.

Two useful approaches for identifying the relevant factors that are responsible for the formation of distribution limits are the use of statistical niche models (Austin, 2007; Holt, 2009) and analysis of phenotypic variation along environmental gradients (Caughley *et al.*, 1988). Statistical niche models establish a statistical relationship between a species distribution, usually in the form of presence–absence data, and a dataset of environmental variables (Austin, Nicholls & Margules, 1990; Peterson, 2001). However, statistical niche models are usually based on coarse-grained data and mainly represent the range of conditions that constitute the realized niche of a species, instead of its fundamental niche, because biotic interactions or dispersal limitation can restrict species from otherwise favourable habitat (Pulliam, 2000; Soberón, 2007). Therefore, the combination of statistical niche models with analyses of phenotypic variation along gradients helps to further isolate potential factors that limit species distributions at finer scales.

Analysing patterns of phenotypic variation along environmental gradients can help tease apart the roles of a phenotypic mismatch to the environment from those of dispersal limitations in the formation of distribution edges. For example, increased levels of physiological stress at the range-margin of the dog-whelk (*Nucella canaliculata*) suggest that gradual changes in temperature and desiccation probability reduce individual fitness and determine the southern range limit of this species (Sorte & Hofmann, 2004). Although this approach does not conclusively determine the specific factor limiting a species' distribution, it is a useful step for identifying candidate variables that impose ecological boundaries (Caughley *et al.*, 1988). In particular, life-history theory constitutes a useful framework for making predictions about phenotypic variation along abiotic and biotic gradients (Roff, 1992; Stearns, 1992; Charlesworth, 1994). Life-history traits (i.e. growth rate, age and size at maturity, reproductive effort, and senescence) are strongly correlated with fitness and therefore influence population dynamics (Cole, 1954). Thus, relevant selection pressures can often be inferred from variation in life-history traits along environmental gradients (Whitehead *et al.*, 2011; Torres-Dowdall *et al.*, 2012). For example, physiological stress as a result of abiotic factors is predicted to decrease reproductive allocation, offspring number, and body condition. By contrast, biotic factors may favour the opposite patterns. For example, increased competition frequently selects for increases in offspring size (Jørgensen, Auer & Reznick, 2011). Therefore, offspring size is expected to increase in localities where closely-related and/or ecologically similar species occur in sympatry relative to allopatric populations. Additionally, increases in extrinsic mortality as a result of predation or parasitism are expected to select for increased reproductive effort and offspring number (Charlesworth, 1994; Torres-Dowdall *et al.*, 2012).

The livebearing fish *Poecilia reticulata* (the Trinidadian guppy) and its sister species *Poecilia picta* (the swamp guppy) are extensively distributed across northern South America and the Caribbean islands (Wischnath, 1993; Breden *et al.*, 1999;

Hrbek, Seckinger & Meyer, 2007). These species are phenotypically similar in morphology and life-history traits and play similar ecological roles (Reznick, Miles & Winslow, 1992). On the island of Trinidad, West Indies, both species can be found in mixed shoals (Magurran & Ramnarine, 2004; Russell *et al*., 2006). Despite both species being recognized as euryhaline (i.e. can tolerate a wide range of salinity; Rosen & Bailey, 1963), only *P. picta* is common in brackish water, whereas *P. reticulata* is more often found in freshwater (Reznick & Endler, 1982; Reznick *et al*., 1992; Wischnath, 1993). This parapatric distribution across the brackish–freshwater interface may reflect secondary contact between these two species because the separation of Trinidad from mainland South-America occurred recently, after the last glacial period (Magurran, 2005). Nevertheless, the distribution limits of these two species across the salinity gradient are unclear because they overlap in parts of their range, and no study to date has quantified the ecological correlates associated with the presence and absence of each species along the salinity gradient. Furthermore, because other factors also vary along lowland rivers of Trinidad (Magurran & Phillip, 2001; Magurran, 2005; Zandonà *et al*., 2011), the specific role of salinity driving the contiguous distribution of these species remains speculative.

In the present study, we took two approaches aiming to understand the distribution limits of *P. reticulata* and *P. picta* along salinity gradients in the lowland sections of Trinidadian rivers. First, we used a statistical niche modelling approach based on the presence/absence data of the two species from 91 localities along the lowland rivers of Trinidad aiming to determine the range of salinity, dissolved oxygen, pH, and elevation each species occupies. Second, we studied the pattern of phenotypic variation of specific traits along these gradients, focusing on fecundity, reproductive allocation, condition, and body size. We sampled *P. reticulata* and *P. picta* from the centre and edge of their distribution in four different drainages aiming to determine the generality of our results.

MATERIAL AND METHODS

COLLECTION SITES AND ENVIRONMENTAL VARIABLES

The study area comprises the lowland rivers of Trinidad, West Indies (Fig. 1). The most conspicuous factor varying along the lowland rivers is salinity. However, several biotic factors also change predictably along the longitudinal section of rivers in Trinidad. First, there appears to be an increase in food resource base for guppies, where the quantity and quality of food
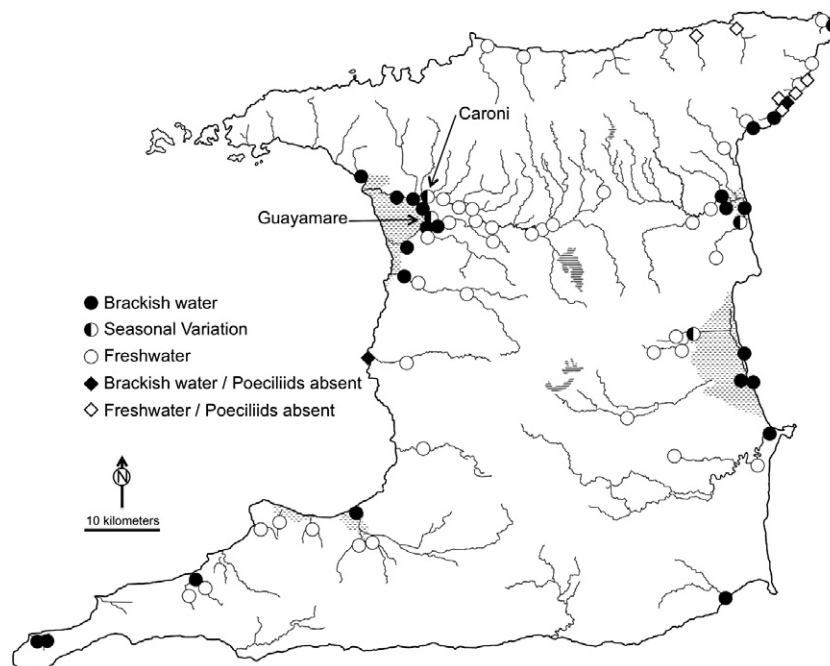

Figure 1. Map of Trinidad indicating the position of the sampled locations. Black dots indicate localities where water was brackish when it was surveyed, and white dots indicate localities where water was fresh. Localities where seasonal variation was observed are marked by a divided dot. The localities at the Caroni River and the Guayamare River indicated on the map were sampled on eight different occasions (four occasions in the wet season and four in the dry season). The few locations where neither *Poecilia reticulata* nor *Poecilia picta* were found are indicated by diamond symbols.

Table 1. Temporal variation in salinity and occurrences of *Poecilia picta* and *Poecilia reticulata* at the interface between fresh and brackish water in the Caroni and Guayamare Rivers

| | | Guayamare River | | | Caroni River | | |
| | | W10.59609, W61.42141 | | | N10.61813, W61.42884 | | |
Date (month/year)	Season	Salinity (ppt)	*Poecilia picta*	*Poecilia reticulata*	Salinity (ppt)	*Poecilia picta*	*Poecilia reticulata*
May 2008	Dry	**2**	**Present**	**Absent**	**5**	**Present**	**Absent**
October 2008	Wet	0	Present	Present	0	Present	Present
January 2009	Wet	**10**	**Present**	**Absent**	**1.5**	**Present**	**Absent**
March 2009	Dry	**5**	**Present**	**Absent**	0	Present	Present
July 2009	Wet	0	Present	Present	0	Present	Present
April 2010	Dry	**40.6**	**Present**	**Absent**	**2.7**	**Present**	**Absent**
August 2010	Wet	0	Present	Present	0	Present	Present
February 2011	Dry	0	Present	Present	**2**	**Present**	**Absent**

Bold text indicates sampling occasions where water was brackish.

resources increase from less productive upstream tributaries to more productive downstream river localities (Zandonà *et al*., 2011). At the freshwater–brackish water interface, rivers are very wide and eutrophication is common compared to upstream sites where only *P. reticulata* is present (WRA, 2001). In addition, there is a dramatic increase in mysid shrimp (*Metamysidopsis* spp.) abundance in the brackish waters where *P. picta* occurs (Mohammed, 2005), suggesting that food might not be limiting in this environment, although it might be a limiting factor further upstream. Second, the complexity of fish communities also changes along the longitudinal profile of rivers (Winemiller & Leslie, 1992). Downstream communities become more diverse as rivers become larger and more productive, potentially increasing interspecific competition, predation risk, and other biotic factors (Magurran & Phillip, 2001; Magurran, 2005). Although few detailed studies have been carried out across the freshwater–brackish water interface in Trinidad, there is evidence that predation pressure increases when moving downstream (Endler, 1995). This is particularly the case for small fish such as guppies because piscivorous fish become more common and abundant at the freshwater–brackish water interface where the fish communities of these two environments meet (Gilliam, Fraser & Alkins-Koo, 1993; Phillip & Ramnarine, 2001).

Between 2008 and 2010, we made 91 collections at 75 locations (most locations sampled only once and four sites sampled on multiple occasions) throughout Trinidad, representing both fresh and brackish water habitat (Fig. 1). We deliberately sampled multiple locales along each river to determine the lowland distribution limits of *P. reticulata* and *P. picta*. Sites close to the brackish–freshwater interface were visited on multiple occasions. In particular, we sampled two sites, one at the Guayamare River and another at the Caroni River, on eight different occasions, including four times during the wet season (June to January) and four during the dry season (February to May; Fig. 1). These sites showed temporal variation in salinity levels, alternating between being fresh during the wet season and brackish during the dry season in response to the freshwater discharge generated by rainfall (Table 1).

The habitat of both species is very similar because they are conspicuously concentrated along the shallow waters near the shore. We determined the presence or absence for each species at each site by actively sampling the shores of the rivers using net sweeps. We maintained a constant sampling effort across all sites, searching for fish over a 30-min period. At all sites, the presence or absence of the two species was relatively easy to quantify, with only the abundance of each species varying. We collected a minimum of 100 fish to determine species composition and chose to standardize our effort by the total number of fish captured rather than a constant time because capture rates varied significantly among localities as a result of factors other than species abundance (e.g. stream access, slope of the shore, substrate of the channel or coastal vegetation). All fish were classified as *P. picta* or *P. reticulata* and, subsequently, were released at their site of capture. At all sample sites, we recorded salinity, geographical coordinates, and elevation. At a subsample of these sites ($N = 42$), we also recorded dissolved oxygen and pH using either an YSI 85 or an YSI ProPlus (YSI Inc.).

To quantify phenotypic differences among localities in life-history traits, four different rivers (Caroni, Caparo, Nariva, and Guayamare) were sampled in April 2010. In each river, upstream, midstream, and downstream sites were selected and 40–60 fish of each species (an approximately 1 : 1 sex ratio) were sampled. These three stream localities represented: (1) a freshwater–upstream locality where only *P. reticulata* occurred; (2) a freshwater–midstream locality where both species were present; and (3) a brackish water–downstream locality where only *P. picta* occurred. However, because there was a very low density of *P. picta* in the Caparo River, we did not sample *P. picta* in this river as a result of worries that we may negatively impact the population. Upon capture, fish were immediately euthanized with an overdose of MS-222 (Argent Laboratories) buffered to a neutral pH with $NaHCO_3$ and preserved in 5% formalin.

We characterized phenotypic variation in life-history traits of wild populations of both species following Reznick & Endler, (1982) and Reznick, Rodd & Cardenas (1996). Briefly, we dissected each formalin-preserved female from our field collection, removed the gastrointestinal tract, and dried the somatic and reproductive tissues, including developing embryos, in a drying oven at 80 °C until mass was stable. From these females we measured: (1) the number of developing embryos and their developmental stage (following Haynes, 1995); (2) the mean dry mass of developing embryos; and (3) reproductive allocation. Mean dry mass of developing embryos was estimated by dividing the total mass of the brood by the number of embryos. Reproductive allocation was quantified as the dry mass of the brood divided by the sum of the dry masses of the somatic tissue of the female and of the brood. Reproductive allocation is thus the proportion of the total dry mass of the mother that consisted of developing embryos. For males, we determined male size at maturity as the mean standard length of adult males, given that males have determinate growth with an asymptote around sexual maturity (Reznick, 1990).

To compare body condition among localities, we used the relative condition index (LeCren, 1951). We estimated relative condition index by species and sex because both study species are sexually dimorphic (i.e. females are larger than males). We estimated condition by first calculating the intercept (a) and the slope (b) of the least squares regression of log-transformed individual mass (M_i) on log-transformed individual length (L_i), and then used these values to calculate predicted mass ($M_i^* = aL_i^b$). Finally, an individual's index was estimated as the ratio of the observed individual mass to the predicted mass (LeCren, 1951; Peig & Green, 2010).

STATISTICAL ANALYSIS

All the analyses were performed separately for *P. reticulata* and *P. picta* because our intention was not to directly compare the species to each other but rather to test the factors that determine the distribution of each species. The only exception is the comparison of life-history traits of these two species in the three freshwater sites where they coexist (see below). The normality and homoscedasticity of the residuals were evaluated and met for all linear models. All analyses were performed using JMP, version 9 (SAS Institute Inc.). All the data used in these analyses have been made publicly available through Dryad (Torres-Dowdall et al., 2013).

STATISTICAL NICHE MODEL

We constructed logistic models based on physicochemical variables (dissolved oxygen, pH, and salinity) and elevation. Elevation is usually used as an indirect variable to the study of distributions as it correlates with several other variables (Austin, 2007). In the present study, elevation was preferred as a spatial explanatory variable over distance from the river mouth for several reasons. First, because the brackish–freshwater interface changes seasonally and the magnitude of this change is associated with elevation, it better represents the probability of brackish water intrusion into lowland rivers. Second, channel size, canopy cover, and community composition gradually change with elevation, potentially affecting the likelihood of finding each species. Finally, analyses including distance to the river mouth did not change our conclusions (not shown).

We considered linear, symmetrical unimodal or skewed responses of the species to the environmental gradients by including linear, quadratic, and cubic polynomial functions in our models. We only considered a linear effect of elevation because *P. reticulata* is known to occur at higher elevations than those sampled in the present study, whereas *P. picta* is expected to be present at sea level but to decrease upstream. Thus, we only sampled the tails of the distributions of both species. We also included interaction terms between environmental variables (Guisan *et al.*, 2006). For *P. reticulata*, we did not consider interactions between salinity and other variables because this species occurred only at freshwater sites (with one exception, see Results). Thus, the combination of salinity levels higher than 0.5 ppt and other variables did not exist. For *P. picta*, we did not consider the interaction between salinity and elevation because, at higher elevation localities, water is always fresh. Finally, we included a null model (intercept only) to compare to candidate models. These models were contrasted against data from the subset

of sites where all the predictor variables were collected (training data, $N = 35$). We then tested the predictions of the best-supported models for *P. reticulata* and *P. picta* with data from the subset of sites that were not used to evaluate the models (test data, $N = 56$ sites). We treated repeated sampling at the same localities as independent because abiotic condition varied from visit to visit as a result of seasonal changes in salinity and affected the probability of finding the target species.

We used Akaike's information criterion adjusted for small sample size (AIC$_C$) to evaluate the relative importance of competing candidate models for explaining the presence or absence of *P. picta* and *P. reticulata* in the lowland rivers of Trinidad (Burnham & Anderson, 2002). AIC$_C$ scores decrease if the addition of new parameters increases the fit of the model sufficiently to compensate for the penalty cost of adding these parameters (i.e. parsimony criterion; Burnham & Anderson, 2002). We calculated and used Akaike weights (w_i) to rank the candidate models, and report a subset of confidence models including those with at least $1/8*w_i$ of the top model (Burnham & Anderson, 2002). Because none of our models was overwhelmingly supported by our data, we used model averaging to determine the importance of the different factors driving the distribution of *P. reticulata* and *P. picta* (Burnham & Anderson, 2002; Johnson & Omland, 2004). To estimate the parameters of the composite model, we used the confidence subset of models. Reducing the number of models to be combined is recommended because removal of a poorly fitted model can increase estimation accuracy (Yuan & Yang, 2005). However, even when we included all the candidate models, our results were not affected. We calculated the weighted mean for model parameters and 95% confidence intervals using an averaged unconditional SE for each parameter (Burnham & Anderson, 2002). We averaged parameters over all models in the confidence set, setting the parameter $i j$ equal to 0 for variable i if it was not included in model j (Lukacs, Burnham & Anderson, 2010). When performing model averaging for the probability of occurrence of *P. picta*, we did not use the model that included the interaction between elevation and dissolved oxygen because interactive terms can result in inaccurate estimations of main effect parameters. However, the weight contribution of this model was small (Table 2). Finally, we estimated a cumulative Akaike weight to evaluate the overall importance for each parameter by adding the Akaike weights of all models containing such parameters (Burnham & Anderson, 2002). Thus, a given parameter will have a cumulative weight close to 1 if all the best-supported models include it as an explanatory variable and have a cumulative weight

Table 2. Confidence set of candidate models predicting the presence or absence of *Poecilia reticulata* and *Poecilia picta* in lowland rivers of Trinidad

Response variable	Model	K	AIC$_C$	ΔAIC$_C$	w_i
Poecilia reticulata – presence	S	4	17.3	0.0	0.41
	E + S	5	18.9	1.6	0.18
	S + DO	5	19.7	2.4	0.13
	S + pH	5	19.7	2.4	0.12
	E + S + pH	6	21.5	4.2	0.05
	E + S + DO	6	21.5	4.2	0.05
Poecilia picta – presence	E	4	17.7	0.0	0.35
	E + S	5	19.5	1.7	0.15
	E + pH	5	19.7	2.0	0.13
	E + DO	5	20.1	2.4	0.11
	E × DO	6	21.0	3.3	0.07
	E + S + pH	6	21.5	3.7	0.05
	E + S + DO	6	21.9	4.1	0.04

Explanatory variables include elevation (E), salinity (S), dissolved oxygen (DO), and pH. *K* indicates the number of parameters, w_i is Akaike weight. AIC$_C$, Akaike's information criterion adjusted for small sample size.

close to 0 if it is not included as an explanatory variable in the set of best-supported models.

SPATIAL PATTERNS OF INTRASPECIFIC LIFE-HISTORY VARIATION

We analyzed *P. picta* and *P. reticulata* life-history data separately using analyses of covariance (ANCOVA), including type of locality of origin (hereafter 'locality') and drainage as categorical fixed effects. Locality represents a comparison between upstream and downstream collections inhabited by each species (see description of stream localities above). We did not consider female size as an informative trait in the present study because females have indeterminate growth. Thus, the size of wild-caught females confounds the effects of age and of the environmental conditions affecting growth. However, fecundity in guppies has been shown to increase with female size; thus, we included female standard length as a covariate for determining reproductive allocation, offspring number, and offspring size (Reznick *et al.*, 1996). We also included the stage of development as a covariate when analysing embryo weight and reproductive allocation because offspring weight decreases as development progresses (Reznick & Endler, 1982). Interactions between covariates and main effects were not significant (all $P > 0.05$); therefore, they were dropped from the final linear models.
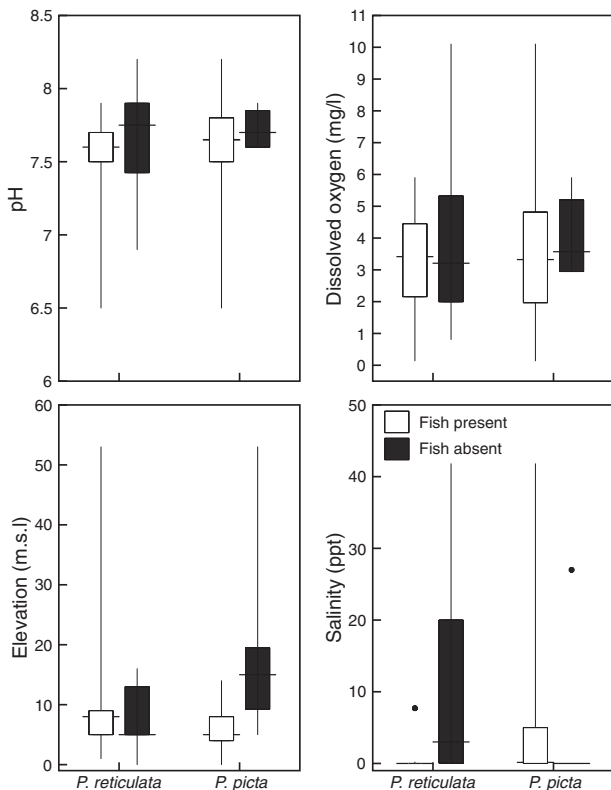
Figure 2. Median, interquartile range, total range of pH, dissolved oxygen, elevation, and salinity at which *Poecilia reticulata* and *Poecilia picta* are present (white bars) or absent (black lines) in lowland rivers of Trinidad. Two outliers are shown for salinity.

INTERSPECIFIC PHENOTYPIC VARIATION BETWEEN *P. RETICULATA* AND *P. PICTA*

We compared *P. reticulata* and *P. picta* life-history traits in sites where they co-occur using ANCOVA, including species and drainage as categorical fixed effects. For the analyses of spatial variation, we included female standard length as a covariate for determining species differences in offspring size, and stage of development as a covariate for analysing embryo weight.

RESULTS

STATISTICAL NICHE MODEL

Poecilia reticulata

Poecilia reticulata was present in 44 of the 91 field collections and the only factor that consistently differed between sites where *P. reticulata* is present or absent was salinity (Fig. 2). We observed some temporal variation in the presence of *P. reticulata* at the two sites that we sampled multiple times (i.e. Caroni and Guayamare Rivers at the brackish–freshwater interface) because this species was present at these sites only when water was fresh, which coincides with the wet season when river discharge is high (Table 1).

Salinity had a negative effect on the probability of finding *P. reticulata*, resulting in an abrupt distribution limit at the brackish–freshwater interface (Fig. 3). Salinity was a significant explanatory variable in all models in the confidence set (Table 2), and salinity had a cumulative weight across all models close to 1 (Table 3). There was little evidence that
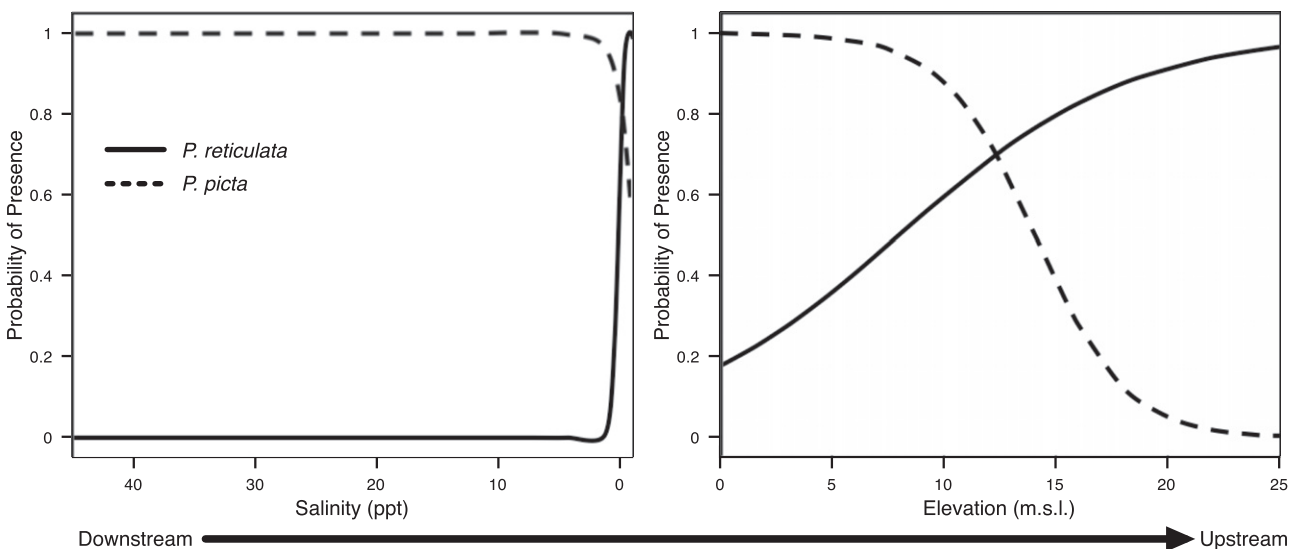

Figure 3. Probability of presence curves for *Poecilia reticulata* (solid lines) and *Poecilia picta* (dashed lines) against salinity (left) and elevation (right). Note that the *x*-axis of salinity (left) proceeds from high to low salinity to be congruent with elevation (left).

Table 3. Model-averaged parameter estimates, their unconditional SEs, and 95% confidence intervals (95% CI) for a composite model predicting the presence or absence of *Poecilia reticulata* and *Poecilia picta* in lowland rivers of Trinidad

Response variable	Parameter	Estimate	SE	95% CI Lower	95% CI Upper	Cumulative w_i
Poecilia reticulata – presence	E	0.043	0.117	−0.186	0.273	0.299
	S	−25.310	11.718	−48.276	−2.343	0.999
	pH	0.024	1.212	−2.351	2.399	0.225
	DO	0.012	0.288	−0.554	0.577	0.225
Poecilia picta – presence	E	−0.496	0.211	−0.909	−0.082	0.999
	S	0.736	4.507	−8.099	9.570	0.277
	pH	−0.413	1.707	−3.759	2.933	0.275
	DO	0.005	0.207	−0.401	0.411	0.268

Explanatory variables include elevation (E), salinity (S), dissolved oxygen (DO), and pH. Cumulative w_i represent the sum of the Akaike weights from all the models that included the explanatory variable.

elevation, dissolved oxygen or pH had any effect on the probability of *P. reticulata* being present at a given site (Figs 2, 3, Table 3). Therefore, we based our predictions of the presence or absence of *P. reticulata* on the set of independent localities using only the best-supported model because it accounted for 41% of the total weight (Table 2), and salinity was the only significant variable in the composite model (Table 3). This model predicted the presence or absence of *P. reticulata* with an overall error rate of 18%. Out of the 34 sites that were predicted to have *P. reticulata* present, it was absent at only nine localities (one river on the southwest peninsula in St Patrick, and eight rivers in the north-east part of the island). The model predicted *P. reticulata* to be absent at 22 sites; however, we did find this species in a brackish site at the Caparo River.

Poecilia picta
Poecilia picta was present in 63 of the 91 samplings and no temporal variation was observed at the brackish–freshwater interface, independently of changes on salinity. *Poecilia picta* is found over a wider range of physicochemical characteristics (Fig. 2). However, in Trinidad, it appears to be limited to sections of the river at low elevation (Fig. 3). Indeed, elevation was a significant variable in all the models in the confidence set (Table 2) and had a cumulative weight close to 1 (Table 3).

Poecilia picta was found at most sites below 10 m a.s.l. However, above 10 m, the probability of finding this species significantly decreased for every meter of increase in elevation (Fig. 3, Table 3). There is no evidence for the effects of salinity, dissolved oxygen, and pH on the probability of presence of *P. picta* (Table 3). As with *P. reticulata*, to predict the presence or absence of *P. picta* at the independent localities, we

used the best-supported model (Table 2) because elevation was the only significant variable in the composite model (Table 3), and the model with just elevation as an explanatory variable accounted for 35% of the total weight (Table 2). This model had an overall error rate of 14%. Of the 41 sites that were predicted to have *P. picta* present, it was actually absent at seven sites (the highly polluted Couva Downstream, two rivers on the southwest peninsula in St Patrick, and four rivers in the north-east part of the island). *Poecilia picta* was absent at all sites where it was predicted to be absent, except at an Oropuche tributary where it was found at 14 m a.s.l.

SPATIAL PATTERNS OF INTRASPECIFIC LIFE-HISTORY VARIATION

Poecilia reticulata
Overall, fish from upstream and downstream localities across the lowland sections of Trinidadian rivers showed no differences in life-history phenotypes. There was a trend for offspring size to be larger in downstream compared to upstream localities, although this was not statistically significant (Fig. 4, Table 4). Male condition varied among localities, with fish being in better condition downstream on all rivers, except on the Caroni River where the pattern was reversed (Fig. 5, Table 4). This tendency for Caroni male fish to be in poorer condition downstream was also observed in females (Fig. 4). Most of the phenotypic variation observed in *P. reticulata* could be explained by intrinsic differences among rivers (Table 4).

Poecilia picta
Intraspecific variation among localities was observed only for offspring size and male size at maturity
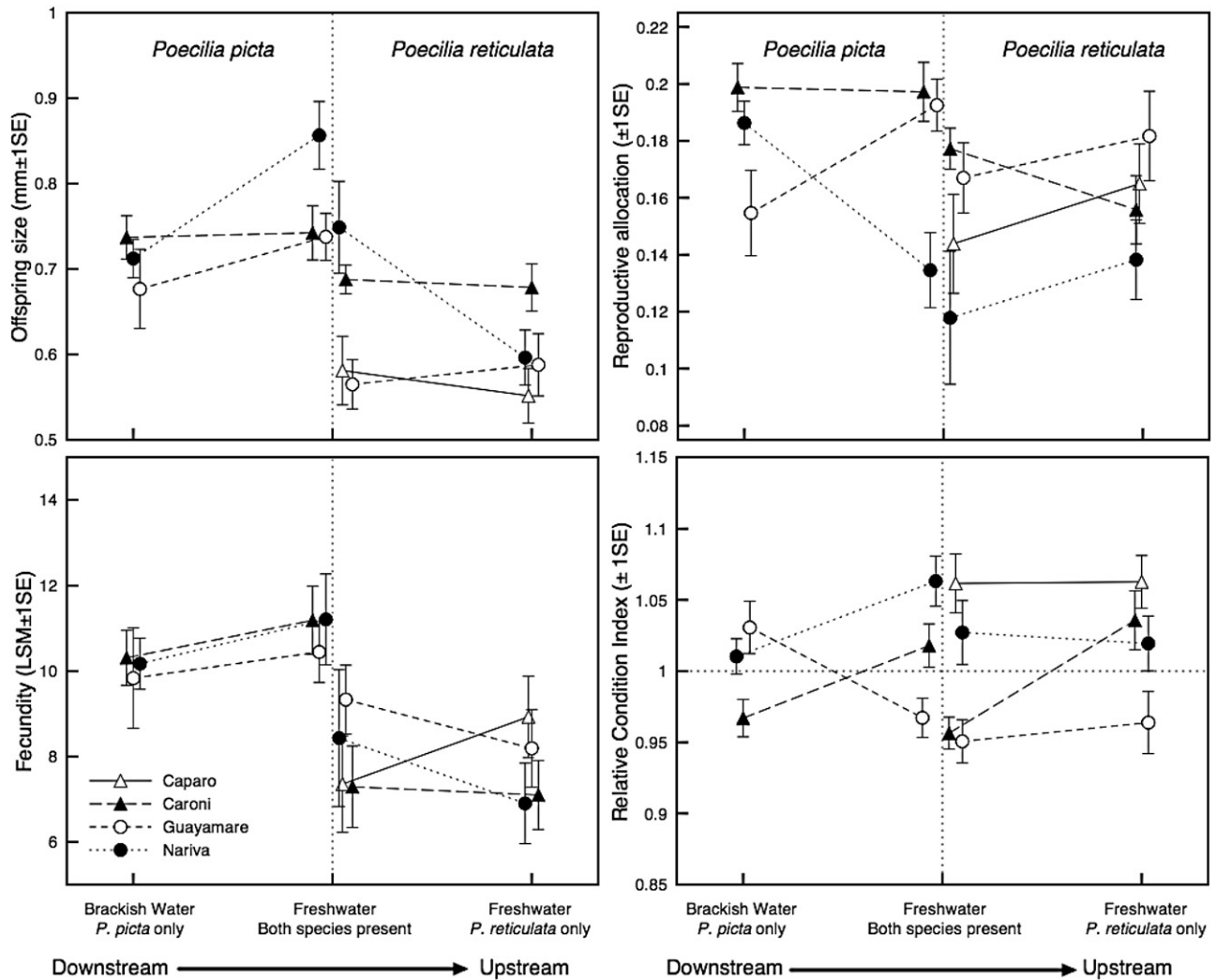
Figure 4. Phenotypic variation in *Poecilia reticulata* and *Poecilia picta* females along longitudinal gradients in lowland rivers in Trinidad. Localities on the left represent *P. picta* only, brackish water sites; localities on the right are *P. reticulata* only, freshwater sites; and the localities in the middle are freshwater sites where both species co-occur.

(Table 4). Overall, females from upstream, freshwater sites produced larger offspring than those from downstream, brackish sites (Fig. 4). Males were larger in downstream brackish sites than in upstream freshwater sites (Fig. 5). Reproductive allocation and female condition depended on the river analyzed and the locality within rivers (Table 4). Female reproductive allocation did not vary among localities in the Caroni River and was higher for freshwater females in the Guayamare River, although it was lower for freshwater females in the Nariva River (Fig. 4). Females from the Caroni and the Nariva rivers were in better condition in upstream freshwater sites, although females from the Guayamare River were in poor condition at the freshwater site (Fig. 4).

INTERSPECIFIC LIFE-HISTORY VARIATION

Poecilia reticulata and *P. picta* did not differ in reproductive allocation in sites where they co-occur ($F_{1,128} = 2.1063$, $P = 0.1491$). Differences among drainages were apparent but interspecific patterns were qualitatively consistent within each drainage (drainage effect: $F_{2,128} = 6.1601$, $P = 0.0028$; interaction: $F_{2,128} = 0.0097$, $P = 0.9903$). However, *P. picta* produced, on average, larger offspring than *P. reticulata* when controlling for developmental stage (least squared mean ± SE: 0.7730 ± 0.0206 and 0.6650 ± 0.0246 mg respectively; $F_{1,128} = 11.3608$, $P = 0.001$). Although the size of the offspring varied among drainages, fish from all drainages showed a similar pattern (drainage effect: $F_{2,128} = 6.1601$, $P = 0.0028$; main

Table 4. Statistical results (F-ratios) from the analysis of covariance on fecundity, reproductive allocation, offspring mass (mg), and the relative condition of wild caught females, and the relative condition and size at maturity of wild caught males

	d.f.	Fecundity	Reproductive allocation	Offspring size	Female relative condition	Male relative condition	Male size
Poecilia picta							
Size	1	161.7221****	–	–	–	–	–
Stage of development	1	–	11.5670****	19.1479****	–	–	–
Locality‡	1	1.4459n.s	0.3303 (NS)	6.9427**	1.1689 (NS)	0.9658 (NS)	20.2088***
Drainage	2	0.2690n.s	4.2127*	2.5854n.s	5.0518**	1.5958 (NS)	18.4793***
Interaction (ExD)	2	0.0266 (NS)	5.1522**	2.5968 (NS)	8.9220****	0.4300 (NS)	2.5640†
Residual sums of squares (d.f.)		1818.1369 (135)	0.2823 (135)	2.6893 (135)	1.5019 (202)	1.6416 (181)	293.1722 (187)
Total sums of squares (d.f.)		4221.3873 (141)	0.3596 (141)	3.3836 (141)	1.7211 (207)	1.6934 (186)	374.9372 (192)
r^2		0.57	0.21	0.21	0.13	0.03	0.22
Poecilia reticulata							
Size	1	151.4042****	–	–	–	–	–
Stage of development	1	–	4.1345*	14.4071****	–	–	–
Locality‡	1	0.2129 (NS)	0.4925 (NS)	2.9341†	2.5386 (NS)	9.0961**	1.5586 (NS)
Drainage	3	1.4272 (NS)	2.9081*	7.9291****	10.6228****	18.1584****	33.5252***
Interaction (ExD)	3	0.8722 (NS)	1.3387 (NS)	1.7569 (NS)	2.4851†	16.0236****	1.0706 (NS)
Residual sums of squares (d.f.)		1745.5382 (141)	0.3535 (133)	0.1.9129 (133)	1.8831 (220)	2.4982 (227)	209.8810 (235)
Total sums of squares (d.f.)		4062.5933 (149)	0.4021 (141)	2.7711 (141)	2.3422 (227)	3.4691 (234)	314.7129 (242)
r^2		0.57	0.12	0.31	0.20	0.28	0.33

†$0.1 > P > 0.05$; *$0.05 > P > 0.01$; **$0.01 > P > 0.001$; ***$P < 0.001$.
‡Locality refers to differences between up, mid, and downstream locales for the study species. NS, not significant.
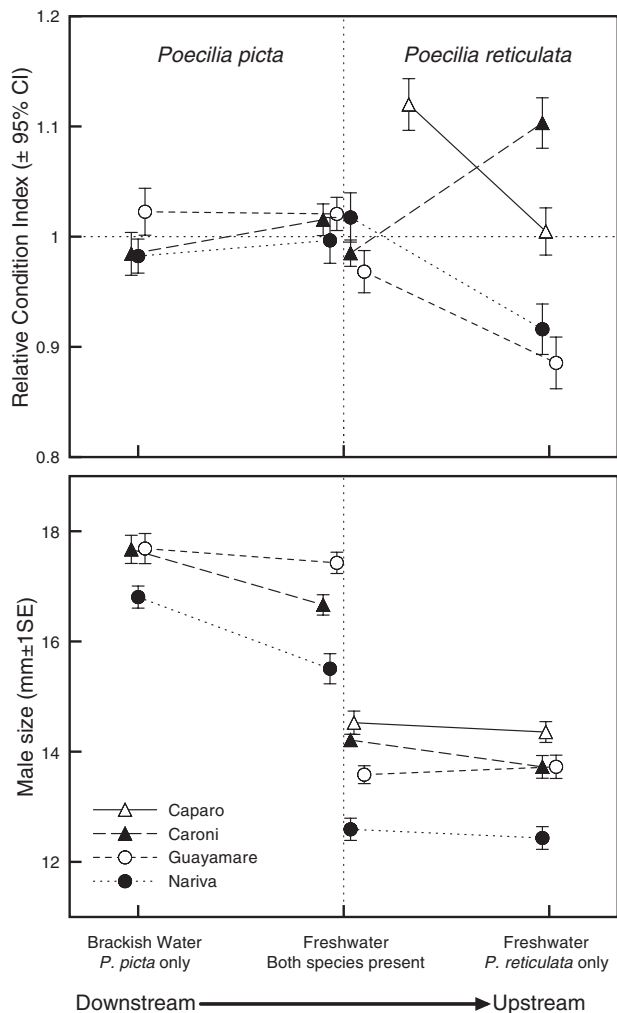
Figure 5. Relative condition and size at maturity *of Poecilia reticulata* and *Poecilia picta* males along lowland rivers in Trinidad. Localities on the left represent *P. picta* only, brackish water sites; localities on the right are *P. reticulata* only, freshwater sites; and the localities in the middle are freshwater sites where both species co-occur.

effects interaction: $F_{2,128} = 0.0097$, $P = 0.9903$; all interactions with the covariate were not significant, $P > 0.05$). Nonetheless, *P. picta* had a lower fecundity than *P. reticulata* when controlling for female size (least squared mean ± SE: 7.1565 ± 0.5064 and 9.4128 ± 0.6131 embryos, respectively; $F_{1,126} = 7.3972$, $P = 0.0075$). Again, there was a drainage effect and, although the interaction was not significant, the difference between species was less evident in the Guayamare drainage (drainage effect: $F_{2,126} = 3.8991$, $P = 0.0228$; main effects interaction: $F_{2,126} = 2.8510$, $P = 0.0615$; all interactions with the covariate were not significant, $P > 0.05$). Differences between

P. picta and *P. reticulata* in the size of mature males varied among rivers. Although *P. picta* males were always larger, the difference was more pronounced in the Guayamare drainage than in the other two drainages (species effect: $F_{2,239} = 361.7872$, $P < 0.0001$; drainage effect: $F_{2,239} = 27.1539$, $P < 0.0001$; interaction: $F_{2,239} = 8.5371$, $P < 0.0003$).

DISCUSSION

Poecilia reticulata and *P. picta* show a contiguous distribution pattern in the rivers of Trinidad, with a zone of overlap in the lowland, freshwater sections. Both species occupy a wide range of pH and dissolved oxygen, as previously reported for *P. reticulata* (Magurran & Phillip, 2001). However, different factors appear to limit the distribution of these two species. On the one hand, *P. reticulata* is primarily limited to the freshwater sections of the rivers, and the probability of it being present rapidly declines as salinity departs from 0 ppt (Fig. 3). The only exception to this pattern was observed in the Caparo River, where *P. reticulata* was found in brackish water. This site was unique because a bridge formed an artificial barrier that resulted in an immediate transition from fresh (0 ppt) to brackish water (7.7 ppt). Although *P. reticulata* was found below the barrier bridge, the species dropped out within the first 50 m of brackish water. On the other hand, the distribution of *P. picta* is limited to the lowlands of Trinidad, and is rarely found over 10 m a.s.l. but occupies both brackish and freshwater.

The statistical niche models based on salinity and elevation performed relatively well in predicting the presence or absence of *P. reticulata* and *P. picta*, respectively. Most erroneous predictions were false positives (i.e. the species was predicted to be present at localities where it was not observed), which is a common error of statistical niche models in cases where the realized niche of a species is smaller than its fundamental niche as a result of biotic interactions or dispersal limitations (Pulliam, 2000; Soberón, 2007). For example, the false positives observed for *P. reticulata* were mainly associated with sites in the north-eastern part of Trinidad, where the species is uncommon (Magurran & Phillip, 2001). Some of these sites might be suitable for guppies, as exemplified by the successful introduction of this species in rivers where it was previously absent (Gordon *et al.*, 2009). This suggests that the realized niche of *P. reticulata* in Trinidad is smaller than its fundamental niche, probably as a result of dispersal limitation.

Water salinity is expected to play a fundamental role shaping species distribution because maintaining water balance is a major physiological challenge

for aquatic species (Nordlie *et al*., 1991; Bœuf & Payan, 2001). Indeed, empirical studies often find that community composition changes significantly along salinity gradients (Martin, 1988; Gelwick *et al*., 2001; Jaureguizar *et al*., 2004; Fuller, McGhee & Schrader, 2007). However, these predictions do not necessarily extend to poeciliid fishes, which are considered to be euryhaline (Rosen & Bailey, 1963), and several species, including *P. reticulata*, show tolerance to gradual changes in salinity (Gibson & Hirst, 1955; Zimmerer, 1983; Shikano & Fujio, 1997). Thus, the abrupt limit to the distribution of this species at the brackish–freshwater interface was unexpected. Nevertheless, two lines of evidence support the importance of salinity in creating the observed pattern of distribution of *P. reticulata*. First, if the distribution limit of this species were caused by gradual changes in unmeasured factors such as predation or competition, we would have expected parallel changes in life-history traits. Instead, we observed no variation in life-history traits between upstream and downstream populations, suggesting an abrupt change in environmental conditions at the distribution limit (i.e. a physiological threshold; Caughley *et al*., 1988). Alternatively, it could be that the environment does gradually change, although *P. reticulata* is unable to adapt to the local optimum along the gradient because gene flow swamps the ability for local adaptation (García-Ramos & Kirkpatrick, 1997). Although we cannot rule out this hypothesis, fish were found in better condition in downstream populations compared to upstream populations, and thus swamping as a result of gene flow appears unlikely. A second line of evidence in support of a threshold response comes from the repeated sampling of localities at the interface between brackish and freshwater in the Caroni and the Guayamare Rivers (Table 1). We only found *P. reticulata* at these localities when water was found to be fresh (i.e. 0 ppt), which mainly coincides with the rainy season. Thus, *P. reticulata* appears to track seasonal changes in salinity and behaviourally avoid brackish water. Behavioural avoidance is expected to evolve if the ecological conditions found outside of the distribution limits consistently result in reduced fitness (Holt, 2003). For example, behavioural avoidance of low-salinity water in echinoderm larvae is adaptive because mortality rapidly increases as salinity falls below seawater levels (Sameoto & Metaxas, 2008). Similarly, behavioural avoidance of brackish water could explain the abrupt distribution limit of *P. reticulata*, providing a proximate explanation to the observed distribution pattern of this species.

By contrast to *P. reticulata*, we found several lines of evidence suggesting that salinity plays only a minor role on driving the distribution of *P. picta* (Fig. 1, Table 2). First, *P. picta* occupies a wide range of salinities, given that it is commonly found at brackish and freshwater localities. Second, we found no signs of physiological stress in life-history traits or condition index when comparing populations from brackish and freshwater localities (Table 4). Finally, the repeated sampling of localities at the brackish–freshwater interface in the Caroni and the Guayamare Rivers also suggests that salinity alone does not explain the distribution of *P. picta*, as we always found this species at those localities independently of the salinity level (Table 1). Nonetheless, *P. picta* was limited to elevations below 10 m a.s.l.

We do not think that elevation per se directly causes *P. picta* distribution limit; rather, we view this as an indirect metric that captures the joint effects of several unmeasured factors that correlate with elevation. First, locations below 10 m a.s.l. are potentially more influenced by tidal changes, and brackish and freshwater are more likely to mix with each other seasonally, thus providing a dynamic environment *P. picta* can tolerate. Second, factors such as productivity and competition are known to change along the elevation gradient (Magurran, 2005). For example, interspecific competition is one likely mechanism limiting the upstream distribution of *P. picta* because offspring size increases from *P. reticulata*-absent localities to *P. reticulata*-present localities (Price & Kirkpatrick, 2009). Larger offspring size has previously been associated with increased competition (Bashey, 2008; Jørgensen *et al*., 2011). Competition intensity between *P. reticulata* and *P. picta* could be intensified in upstream localities as a result of the reduced primary productivity caused by increased canopy cover observed in Trinidad streams (Reznick, Butler & Rodd, 2001; Zandonà *et al*., 2011). Lastly, predation is likely to change along the elevational gradient in a manner that could shape the distributional limits of *P. picta*. Increased mortality as a result of predation is expected to select for faster life histories (Charlesworth, 1994). Reznick *et al*.(1992) described *P. picta* as a poeciliid that is adapted to extremely high levels of predation based on their fast life histories. Indeed, *P. picta* has faster life histories than upstream populations of *P. reticulata* populations (Reznick *et al*., 1992; Torres-Dowdall *et al*., 2012; present study). However, we did not find *P. picta* to have a faster life history than sympatric, downstream populations of *P. reticulata*. Indeed, *P. picta* females produced fewer, larger offspring than *P. reticulata* females, and *P. picta* males matured at a larger size than *P. reticulata* males at sites where they co-occur. Thus, it appears that the ability of *P. picta* to cope with very high levels of predation risk occurs through the use of a completely different strat-

egy than that used by *P. reticulata* (Chase, 1999; Abrams, 2000). For example, although *P. reticulata* has adapted to increased predator induced mortality by increasing reproductive output, *P. picta* may persist through an increased ability to escape predators. Preliminary results from laboratory experiments suggest that *P. picta* might have a higher probability of escaping pike cichlid (*Crenicichla frenata*) strikes than *P. reticulata* (J. Torres-Dowdall, personal observations). Therefore, *P. picta* might exhibit behaviours that result in lower mortality rates than *P. reticulata* for a given level of predation risk (Lima & Dill, 1990).

In summary, we describe a pattern of contiguous distribution along a salinity gradient in the rivers of Trinidad for two closely-related and morphologically similar species of poeciliid fish, *P. picta* and *P. reticulata*. *Poecilia picta* occupies the estuarine end of the gradient, spanning a wide range of salinities (Fig. 3). However, it is also found in the lowland, freshwater sections of rivers, where it co-occurs with *P. reticulata*. On the other end of the gradient, the distribution of *P. reticulata* begins in freshwater localities and extends further upstream than *P. picta*. Our results suggest that different mechanisms might be responsible for the distribution limits of the two focal species, although further experiments are needed to confirm these mechanisms. This type of asymmetric pattern, where different factors are responsible for the replacement of species along a gradient, has been observed in other species. For example, Taniguchi & Nakano (2000) showed that the upstream limit to the distribution of the white-spotted charr (*Salvelinus leucimaenis*) is caused by the low tolerance of this species to low temperatures. However, in the warmer, downstream sections of the streams, it is competitively dominant over the dolly varden (*Salvelinus malma*), displacing this species to the upstream, coldest section of the streams. Similarly in birds, reciprocal removal experiments reveal that the Virginia's warbler (*Vermivora virginiae*) is limited to nesting in a warmer and drier microclimate by the presence of the competitively dominant orange-crowned warbler (*Vermivora celata*), which occupies less stressful, cooler and wetter habitats (Martin & Martin, 2001). In turn, this pattern at the local scale provides an explanation for the pattern at the regional scale where the Virginia's warbler is limited to more arid areas than the orange-crowned warbler. Similarly, our results suggest that, although salinity limits *P. reticulata*, the limits to the distribution of *P. picta* could be driven by interspecific competition. Consistent with previous studies, our survey of *P. picta* and *P. reticulata* suggests that the parapatric distribution of these two species at regional scales is the result of different processes affecting each species at local scales.

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REFERENCES

Abrams PA. 2000. The evolution of predator–prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* **31:** 79–105.

Allan JD, Castillo MM. 2007. *Stream ecology: structure and function of running waters*, 2nd edn. Dordretch: Springer.

Angert AL. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *Proceedings of the National Academy of Sciences of the United States of America* **106: S2:** 19693–19698.

Attrill MJ, Rundle SD. 2002. Ecotone or ecocline: ecological boundaries in estuaries. *Estuarine, Coastal and Shelf Science* **55:** 929–936.

Austin M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* **200:** 1–19.

Austin MP, Nicholls AO, Margules CR. 1990. Measurement of the realized quantitative niche: environmental niches of five Eucalyptus species. *Ecological Monographs* **60:** 161–177.

Bashey F. 2008. Competition as a selective mechanism for larger offspring size in guppies. *Oikos* **117:** 104–113.

Bœuf G, Payan P. 2001. How should salinity influence fish growth? *Comparative Biochemistry and Physiology Part C* **130:** 411–423.

Breden F, Ptacek MB, Rashed M, Taphron D, Figueiredo CA. 1999. Molecular phylogeny of the live-bearing fish genus *Poecilia* (Cyprinodontiformes: Poeciliidae). *Molecular Phylogenenetics and Evolution* **12:** 95–104.

Burnham KP, Anderson DR. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.

Caughley G, Grice D, Barker R, Brown B. 1988. The edge of the range. *Journal of Animal Ecology* **57:** 771–785.

Charlesworth B. 1994. *Evolution in age-structured populations*, 2nd edn. Cambridge: Cambridge University Press.

Chase JM. 1999. To grow or to reproduce? The role of life-history plasticity in food web dynamics. *American Naturalist* **154:** 571–586.

Chase JM, Leibold MA. 2003. *Ecological niches: linking classical and contemporary approaches*. Chicago, IL: The University of Chicago Press.

Chase JM, Myers JA. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **366:** 2351–2363.

Cole LC. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* **29:** 103–137.

Connell JH. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42:** 710–723.

Coulson LA, Perrin C, Roberts DG, Minchinton TE, Ayre DJ. 2011. Can limited dispersal or biotic interaction explain the declining abundance of the whelk, *Morula marginalba*, at the edge of its range? *Biological Journal of the Linnean Society* **103:** 849–862.

Dunson WA, Travis J. 1991. The role of abiotic factors in community organization. *American Naturalist* **138:** 1067–1091.

Endler JA. 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends in Ecology and Evolution* **10:** 22–29.

Fausch KD, Nakano S, Ishigaki K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia* **100:** 1–12.

Fuller RC, McGhee KE, Schrader M. 2007. Speciation in killifish and the role of salt tolerance. *Journal of Evolutionary Ecology* **20:** 1962–1975.

García-Ramos G, Kirkpatrick M. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* **51:** 21–28.

Gaston KJ. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gelwick FP, Akin S, Arrington DA, Winemiller KO. 2001. Fish assemblage structure in relation to environmental variation in a Texas Gulf coastal wetland. *Estuaries* **24:** 285–296.

Gibson MB, Hirst B. 1955. The effect of salinity and temperature on the pre-adult growth of guppies. *Copeia* **1955:** 241–243.

Gilliam JF, Fraser DF, Alkins-Koo M. 1993. Structure of a tropical stream fish community: a role for biotic interactions. *Ecology* **74:** 1856–1870.

Gomes JJL, Monteiro LR. 2007. Size and fecundity variation in populations of *Poecilia vivipara* Block & Schneider (Teleostei; Poeciliidae) inhabiting an environmental gradient. *Journal of Fish Biology* **71:** 1799–1809.

Gordon SP, Reznick DN, Kinnison MT, Bryant MJ, Weese DJ, Räsänen K, Millar NP, Hendry A. 2009. Adaptive changes in life history and survival following a new guppy introduction. *American Naturalist* **174:** 34–45.

Grinnell J. 1917. The niche-relationships of the California thrasher. *Auk* **34:** 427–433.

Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMCC, Aspinall R, Hastie T. 2006. Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology* **43:** 386–392.

Hairston NG. 1949. The local distribution and ecology of the plethodontid salamanders of the Southern Appalachians. *Ecological Monographs* **19:** 47–73.

Hairston NG. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* **61:** 817–826.

Haynes JL. 1995. Standardized classification of poeciliid development for life-history studies. *Copeia* **1995:** 147–154.

Holt RD. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* **5:** 159–178.

Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 19659–19665.

Hrbek T, Seckinger J, Meyer A. 2007. A phylogenetic and biogeographic perspective on the evolution of poeciliid fishes. *Molecular Phylogenenetics and Evolution* **43:** 986–998.

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symposium in Quantitative Biology* **22:** 415–427.

Jaureguizar AJ, Manni R, Guerrero R, Lasta C. 2004. Environmental factors structuring fish communities of the Río de la Plata estuary. *Fisheries Research* **66:** 195–211.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19:** 101–108.

Jørgensen C, Auer SK, Reznick DN. 2011. A model for optimal offspring size in fish, including live-bearing and parental effects. *American Naturalist* **177:** E119–E135.

LeCren ED. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* **20:** 201–219.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68:** 619–640.

Lomolino MV, Riddle BR, Brown JH. 2006. *Biogeography*. Sunderland, MA: Sinauer Associates.

Lukacs PM, Burnham KP, Anderson DR. 2010. Model selection bias and Freedman's paradox. *Annals of the Institute of Statistical Mathematics* **62:** 117–125.

Magurran AE. 2005. *Evolutionary ecology. The Trinidadian guppy*. Oxford: Oxford University Press.

Magurran AE, Phillip DAT. 2001. Evolutionary implications of large-scale patterns in the ecology of Trinidadian guppies, *Poecilia reticulata*. *Biological Journal of the Linnean Society* **73:** 1–9.

Magurran AE, Ramnarine IW. 2004. Learned mate recognition and reproductive isolation in guppies. *Animal Behaviour* **67:** 1077–1082.

Marshall S, Elliott M. 1998. Environmental influences on the fish assemblage of the Humber Estuary, U.K. *Estuarine, Coastal and Shelf Science* **46:** 175–184.

Martin PR, Martin TE. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology* **82:** 189–206.

Martin TJ. 1988. Interaction of salinity and temperature as a mechanism for spatial separation of three co-existing species of *Ambassidae* (Cuvier) (Teleostei) in estuaries on the south-east coast of Africa. *Journal of Fish Biology* **33:** 9–15.

Mohammed A. 2005. Toxicity of water-soluble fractions of four fuels for *Metamysidopis insularies*, an indigenous tropical mysid species. *Environmental Monitoring and Assessment* **104:** 37–44.

Nordlie FG, Walsh SJ, Haney DC, Nordlie TF. 1991. The influence of ambient salinity on routine metabolism in the teleost, *Cyprinidon variegatus* Lacépède. *Journal of Fish Biology* **38:** 115–122.

Peig J, Green AJ. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* **24:** 1323–1332.

Peterson AT. 2001. Predicting species' geographic distributions based on ecological niche modelling. *Condor* **103:** 599–605.

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Bastos Araújo M. 2011. *Ecological niches and geographic distributions*. Monographs in Population Biology 49. Princeton, NJ: Princeton University Press.

Peterson-Curtis TL. 1997. Effects of salinity on survival, growth, metabolism, and behavior in juvenile hogchokers, *Trinectes maculates fasciatus* (Achiridae). *Environmental Biology of Fishes* **49:** 323–331.

Phillip DAT, Ramnarine IW. 2001. *An illustrated guide to the freshwater fishes of Trinidad and Tobago*. St Augustine, FL, Trinidad and Tobago: University of the West Indies.

Poff NL. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16:** 391–409.

Price TD, Kirkpatrick M. 2009. Evolutionary stable range limits set by interspecific competition. *Proceedings of the Royal Society of London, Series B, Biological Sciences* **276:** 1429–1434.

Pulliam HR. 2000. On the relationship between niche and distribution. *Ecology Letters* **3:** 349–361.

Reznick DN. 1990. Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): an experimental evaluation of alternative models of development. *Journal of Evolutionary Biology* **3:** 185–203.

Reznick DN, Endler JA. 1982. The impact of predation on life history evolution in Trinidadian guppies: (*Poecilia reticulata*). *Evolution* **36:** 160–177.

Reznick DN, Miles DB, Winslow S. 1992. Life history of *Poecilia picta* (Poecillidae) from the Island of Trinidad. *Copeia* **1992:** 782–790.

Reznick DN, Rodd FH, Cardenas M. 1996. Life-history evolution in guppies (*Poecilia reticulata:* Poeciliidae). IV. Parallelism in life-history phenotypes. *American Naturalist* **147:** 319–338.

Reznick DN, Butler MJ IV, Rodd FH. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *American Naturalist* **157:** 126–140.

Roff DA. 1992. *The evolution of life histories. Theory and analysis*. New York, NY: Chapman & Hall, Inc.

Rosen DE, Bailey RM. 1963. The poeciliid fishes (Cyprindontiformes), their structure, zoogeography, and systematics. *Bulletin of the American Museum of Natural History* **126:** 1–176.

Russell ST, Ramnarine IW, Mahabir R, Magurran AE. 2006. Genetic detection of sperm from forced copulations between sympatric populations of *Poecilia reticulata* and *Poecilia picta*. *Biological Journal of the Linnean Society* **88:** 397–402.

Sameoto JA, Metaxas A. 2008. Can salinity-induced mortality explain larval vertical distribution with respect to a halocline? *Biological Bulletin* **214:** 329–338.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics* **40:** 415–436.

Shervette VR, Ibarra N, Gelwick F. 2007. Influences of salinity on growth and survival of juvenile pinfish *Lagodon rhomboides* (Linnaeus). *Environmental Biology of Fishes* **78:** 125–134.

Shikano T, Fujio Y. 1997. Successful propagation in seawater of the guppy *Poecilia reticulata* with reference to high salinity tolerance at birth. *Fisheries Science* **63:** 573–575.

Soberón J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10:** 1115–1123.

Sorte CJB, Hofmann GE. 2004. Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca: Gastropoda) is more stressed at its range edge. *Marine Ecology Progress Series* **274:** 263–268.

Stearns SC. 1992. *The evolution of life histories*. New York, NY: Oxford University Press.

Taniguchi Y, Nakano S. 2000. Condition-specific competition: implication for the altitudinal distribution of stream fishes. *Ecology* **81:** 2027–2039.

Torres-Dowdall J, Dargent F, Handelsman CA, Ramnarine IW, Ghalambor CK. 2013. Data from: ecological correlates of the distribution limits of two poeciliid species along a salinity gradient. *Dryad Digital Repository* doi:10.5061/dryad.s1v35.

Torres-Dowdall J, Handelsman CA, Ruell E, Auer S, Reznick DN, Ghalambor CK. 2012. Fine-scale local adaptation in life histories along a continuous environmental gradient in Trinidadian guppies. *Functional Ecology* **26:** 616–627.

Twomey E, Morales V, Summers K. 2008. Evaluating condition-specific and asymmetric competition in a species-distribution context. *Oikos* **117:** 1175–1184.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* **37:** 130–137.

Whitehead A, Roach JL, Zhang S, Galvez F. 2011. Genomic mechanisms of evolved physiological plasticity in killifish distributed along an environmental salinity gradient. *Proceedings of the National Academy of Sciences of the United States of America* **108:** 6193–6198.

Wiens JJ. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **366:** 2336–2350.

Winemiller KO, Leslie MA. 1992. Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environmental Biology of Fishes* **34:** 29–50.

Wischnath L. 1993. A*tlas of livebearers of the world.* Neptune, NJ: TFH Publications, Inc.

WRA. 2001. *Integrating the management of watersheds and coastal areas in Trinidad and Tobago.* Trinidad and Tobago: Water Resource Agency, Ministry of the Environment.

Yuan Z, Yang Y. 2005. Combining linear regression models: when and how? *Journal of the American Statistical Association* **100:** 1202–1214.

Zandonà E, Auer SK, Kilham SS, Howard JL, López-Sepulcre A, O'Connor MP, Bassar RD, Osorio A, Pringle CM, Reznick DN. 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. *Functional Ecology* **25:** 964–973.

Zimmerer EJ. 1983. Effect of salinity on the size-hierarchy effect in *Poecilia latipinna, P. reticulata* and *Gambusia affinis. Copeia* **1983:** 243–245.