Biol Invasions (2015) 17:245–256
DOI 10.1007/s10530-014-0723-0

ORIGINAL PAPER

Limited options for native goodeid fish simultaneously confronted to climate change and biological invasions

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Received: 24 May 2013 / Accepted: 15 May 2014 / Published online: 1 June 2014

Abstract The process by which climate warming promotes the invasive expansion of tropical and subtropical species is commonly studied within the niche conservatism framework, which ignores the possibility of rapid evolution of thermal niche. We demonstrate that competition with the tropical invasive *Pseudoxiphophorus bimaculatus* has led to thermal niche displacement in the temperate fish *Girardinichthys multiradiatus*. Data mining of field records indicates that temperature is the main factor determining which species is dominant, behavioural performance profiles confirmed thermal segregation of these species and laboratory trials demonstrate that *G. multiradiatus* co-occurring with *P. bimaculatus* has shifted their thermal optimum to a lower temperature. An exploration of the consequences of these processes under climate change using a thermodynamic model predicts increased frequency of *P. bimaculatus* with global warming. This reveals a dilemma facing temperate species confronting tropical competitors; the need to adjust their thermal niche to escape competition behind a shrinking cold barrier, a lose–lose situation given current climatic trends.

Electronic supplementary material The online version of this article (doi:10.1007/s10530-014-0723-0) contains supplementary material, which is available to authorized users.

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Keywords Fish invasions · Climate change · Thermal niche · Niche displacement · Data mining · Ecological modelling

Introduction

Warmer conditions favour invasive species from various taxa (Mainka and Howard 2010; Sorte et al. 2010; Song et al. 2010; Clements and Ditommaso 2011; Zerebecki and Sorte 2011; Crossman et al. 2011), creating a synergy between global climatic change and biological invasions that constitutes a major threat to the maintenance of global biodiversity (Thomas et al. 2004; Holzapfel and Vinebrooke 2005; Chown et al. 2007; Pejchar and Mooney 2009). Fish communities in temperate regions, normally dominated by cold-water species, are vulnerable to the effects of warming temperatures. Additionally, they face possible invasions by warm-water fishes capable to colonise new habitats as the thermal constraints on their life histories are relaxed (Britton et al. 2010). These processes are generally assumed to be mediated by thermal niche conservatism (Broennimann et al. 2007; Stebbins 2003; Jarnevich and Stohlgren 2009; Reino et al. 2009), yet the concept that invasive species have largely unchanging thermal niches is at odds with the finding that climatic niche shift has occurred amongst freshwater fish and lizards (Lauzeral et al. 2011; Kolbe et al. 2012).

Models linking climatic change and biodiversity emphasize the effects of increased habitat availability for invasive species, ignoring the possible changes in thermal niche of either invasive or native species. We present evidence of adaptive shifts in the thermal niche to reduce direct competition with an invasive species, and the observation that this shift makes a native species increasingly maladapted to a warming environment. This unexpected twist challenges several aspects of current range shift predictions: the assumptions of (1) thermal niche constancy; (2) limited adaptive responses; and (3) the tendency to ignore synergistic effects of multiple aspects of global change. Poeciliid fishes, which are considered excellent colonizers and invaders (Magurran 2009; Gesundheit and Macías Garcia 2007), have invaded multiple sites in Central Mexico, including the last few remaining localities of some endangered members of the Goodeidae (splitfins). The approximately 41 endemic species of the subfamily Goodeinae, many of which are considered endangered and some already extinct in the wild (Webb et al. 2004; De la Vega-Salazar et al. 2003), constitute a substantial part of the fish fauna of central Mexico. Goodeids are often the only local native fish species, such as the distinct population of the threatened *Girardinichthys multiradiatus* at Zempoala lakes (Macías Garcia et al. 2012), which has been cohabiting with the introduced poeciliid *Pseudoxiphophorus bimaculatus* (Morales-Cazan and Albert 2012) for about 12 years (C. Macías Garcia pers. obs.).

Negative effects resulting from competition for resources are expected, given ecological similarities between *G. Multiradiatus* and *P. bimaculatus*. Both display the same preferences for shaded slow-moving waters at depths no greater than 1 m, and there is substantial diet overlap between them (Trujillo Jiménez and Toledo Beto 2007; Trujillo Jiménez and Espinosa de los Monteros Viveros 2006). As *G. multiradiatus* inhabits cold waters at altitudes from 2,200 to 2,800 m above mean sea level (mamsl) and *P. bimaculatus* is naturally found in warm waters at altitudes below 1,430 mamsl (Fig. 1), coexistence was not expected. This suggests that following the unexpected establishment of the latter at Zempoala, a temperature-mediated interaction between the two species may have ensued.

Fish use of lacustrine habitat is normally constrained by water temperature and concentration of dissolved oxygen (Jiang et al. 2012). Thus, it is likely that shore temperature is a key factor mediating the interactions between *G. multiradiatus* and *P. bimaculatus* at Zempoala. It would be expected that montane *G. multiradiatus*, adapted to colder waters, possesses a thermal advantage over *P. bimaculatus* in its high-altitude habitat. Given the current climatic change, understanding the role of thermal regimes in mediating the interactions between these species is important since a rise in water temperature would eliminate the hypothesized advantage of *G. multiradiatus*.

Here we sought to understand the joint effects of facing an invasive tropical competitor (*P. bimaculatus*) and of (shifting) ambient temperature, on the abundance and distribution of *G. multiradiatus* at the temperate Zempoala lakes. We hypothesised that the sign of the interactions between the two species would be negative, and that their intensity and outcome would be a function of water temperature. In the laboratory, we used standardised behavioural essays to quantify the interactions between the species at different temperatures, and used the data to build thermal performance curves. In the field we conducted monthly censuses at fixed collecting sites from two lakes; one where *P. maculatus* was introduced and one where it is absent. We used a multivariate approach based on machine-learning techniques to evaluate which sequence of rules (i.e. a decision tree; Hand1998) drawn from our limnological descriptions best explained the abundance and distribution of both species. Finally we used coefficients of performance from the laboratory trials, and limnological data, to predict population trends using a thermodynamics-inspired model (Michaelian 2005).

Materials and methods

The poeciliid *P. bimaculatus* was introduced to Zempoala at some time between 1995 and 1997 (C. Macías Garcia pers. obs.). Zempoala is the largest of three (extant) lakes comprising the Lagunas de Zempoala National park, near Mexico City. Lake Zempoala (19°03′00″N–99°18′42″W) lies at an altitude of 2,800 mamsl at the foot of the mount Zempoala It covers between 10.56 ha (dry season) and 12.34 ha (rainy season), with an average depth of 8.0 m (Bonilla-Barbosa and Lases 1997). Less than

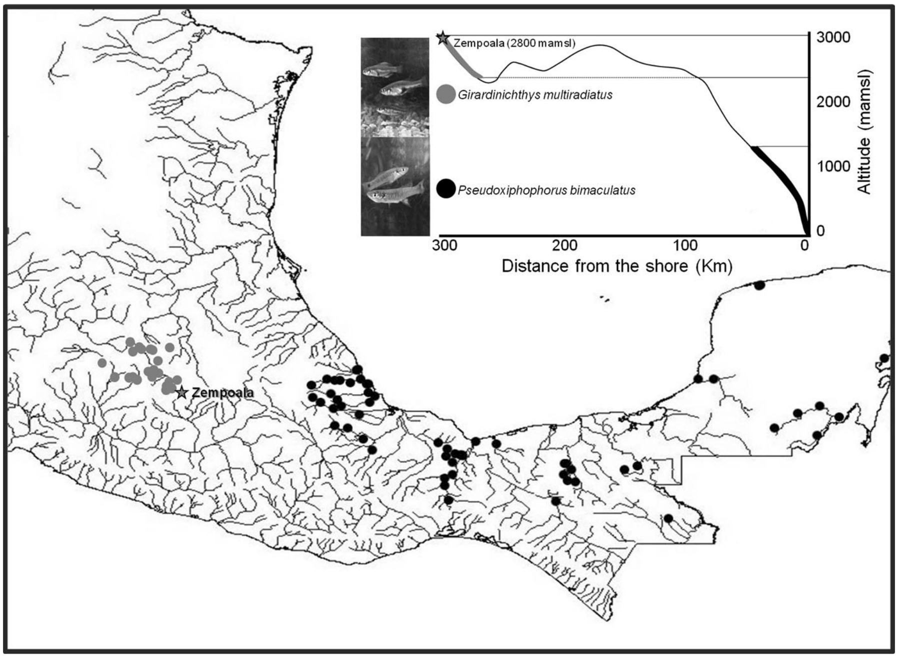

Fig. 1 Native altitudinal ranges of *P. bimaculatus* (*black thick line*) and *G. multiradiatus* (*gray thick line* in the *inset*); *G. multiradiatus* is found exclusively in the highlands of central Mexico (*inset*; altitudinal profile of central Mexico from southern Veracruz to the south of the trans-Mexican volcanic belt), at a lowest altitude some 1,300 m above the highest native populations of *P. bimaculatus*. The native drainages of both species are separated by the mountains of the trans-Mexican volcanic belt

200 meters to the west is the smaller (5.3–6.1 ha) Tonatiahua (19°03′N–99°19’W), at an altitude of 2,810 mamsl between mounts Alumbres and Ocuilan. The only fish native to the national park is *G. multiradiatus*, but exotic rainbow trout (*Oncorhynchus mykiss*) and common carp (*Cyprinus carpio*) have long been established in both Zempoala and Tonatiahua. Both lakes are fed by independent springs, and although they belong to the same national park, they lie at opposite sides of the border between the States of Morelos and Mexico, and are thus managed in somewhat different ways from their respective municipalities. *P. bimaculatus* is present in Zempoala but not in Tonatiahua.

Monthly censuses of fish were conducted for 1 year in both Zempoala and Tonatiahua, beginning in June 2009 and ending in May 2010. We established 14 evenly-spaced sampling sites around Zempoala shores, and 10 along the perimeter of smaller Tonatiahua (an equivalent density of sampling sites considering the lakes perimeters: 1500 m for Zempoala lake and 1150 m for Tonatiahua lake). As *P. bimaculatus* and *G. multiradiatus* preferentially occupy areas between 0 and 1 m from the shore, 10 standardized hauls were made at each site with a square (38 × 38 cm) nylon dip net (handle = 42 cm, mesh = 0.3 cm) within 1 m from the shore. All captured fish were identified, sexed, measured and then released. At each site we measured temperature (°C; HANNA^{TM} HI9146) and dissolved oxygen (ppm; HANNA^{TM} HI9146), and categorised habitat structure according to substrate type (sandy, rocky, mixed), shore slope (gentle, abrupt) and vegetation density (high, low). Additionally, we collected monthly water samples at five sites from each lake to quantify ammonium, nitrites, nitrates, orthophosphates and phosphate (mg/L; HANNA C-200^{TM} HI83200), water turbidity (NTU; HANNA^{TM} HI93703) and pH (Hanna HI1208). The monthly average values of these seven variables were deemed to describe the water quality of all sites within a lake at any given date.

Field data were analysed using data mining (Quinlan 1993; Hand 1998). This is a set of techniques developed to find patterns in large datasets using machine-learning. Machine-learning is the training of an analytical system based on the nature of the data that are analysed, on multivariate statistics and on data-base processing techniques. A usual output of data mining is a decision tree (see below). We processed the field data using the J48 java implementation in WEKA software (Hall et al. 2009) of the C4.5 classification algorithm in order to construct a decision tree that would describe the pathways linking the habitat variables with the abundance of both fish species. Nodes in a decision tree are built using information-gain criteria and represent logical decision rules that can be used to understand causal links between the input (independent variables; i.e. our habitat categories and water quality data) and the response variable (fish abundance). We classified the 168 fish censuses from Zempoala (14 sites sampled 12 times each) into to six categories according to whether we found: (1) only *G. multiradiatus*, (2) only *P. bimaculatus*, (3) a majority (≥70 %) of *G. multiradiatus*; (4) a majority (≥70 %) of *P. bimaculatus*, (5) both species, but neither preponderates, and (6) no fish. The 70 % criterion of preponderance was reached following an analytic hierarchy process (AHP) based on paired comparisons corresponding to a "Very strong importance" in the fundamental scale of pairwise comparisons (see Saaty 2008).

Fish used for thermal profiling were collected at Zempoala (both species) and Tonatiahua (*G. multiradiatus*), and transported in plastic bags containing water from the collection site, protective skin coating (Stress-coat^{TM} or Pentabiocare^{TM}) and antiseptic. In the laboratory fish were separated by sex and kept in 40 L tanks under a 12/12 h photoperiod, fed commercial fish food flakes (SeraVipan^{TM}) twice daily, and maintained at 22 °C until trials began 2–3 weeks later. Behavioural performance was measured at 10, 14, 18, 22 and 26 °C inside a Conviron^{TM} plant growth chamber fitted with a CMP3244 controller, where they were maintained under a 12/12 light/dark schedule and fed twice daily. These temperatures are within the range measured at the shores of Zempoala, and a few pilot trials indicated that at 27 °C *G. multiradiatus* struggled (and a few died during a single pilot trial at 28 °C), whereas at 8 °C *P. bimaculatus* became sluggish/motionless. Focal fish were individually kept in 2-L aquaria for acclimation between test temperatures.

Fish were initially introduced into the chamber at laboratory temperature (22 °C), allowed to acclimate for 3 days, and then the temperature was increased 1 °C/day until reaching the first test temperature (26 °C; the closest to the temperature to which fish had been acclimated in the laboratory). Behavioural performance was then measured after three days of acclimation. Then the temperature was decreased by 1 °C/day until reaching the next test temperature (22 °C), which was followed by a 3-day acclimation period, behavioural tests, and a new gradual reduction of temperature until fish had been tested at all the specified temperatures. This procedure involves a slower rate of temperature shifts than normally used in studies of fish thermal performance curves (Wilson et al. 2001; Schulte et al. 2011), and exposed them to a smaller change of temperature than that measured at the shores of Zempoala within a day (5.07 ± 2.31). All fish exposed to this protocol were returned unharmed to the field.

We conducted four types of trials, in which we measured (1) feeding, or (2) sexual behaviour of *G. multiradiatus* either on their own (allowing only intraspecific interactions) or with *P. bimaculatus* (heterospecific interactions allowed). There were three replicates per type of trial, each involving two male and two female *G. multiradiatus* (n = 12) or one male and one female of each species (interspecific interactions; n = 6 fish per species).

Feeding behaviour

Fish were not fed for 24 h before feeding trials; then they were transferred to the 3-L observation tank, and after 5 min of habituation, a single fish food flake (Sera-Vipan^{TM}) was dropped on the tank every 2 min. For 8 min following the dropping of the first flake we recorded from each fish: latency to nibble the food (one per fish per flake), number of feeding bites and number of feeding events (swallowing a portion of the flake).

Sexual behaviour

First we formed 12 different pairs of similar-sized fish of each species, then we re-assembled them into 12 pairs of fish of different size in order to incorporate the variance due to size differences during fish encounters. Fish, which had been acclimated in individual tanks, were then introduced to a 3-L tank divided into two compartments by a glass partition. Males occupied the front partition and were visually exposed to the females in the back. We measured sexual behaviour as both the frequency and duration of male approaches to females, and simultaneously recorded the frequency and duration of attacks between males.

For demographic projections under different climate warming scenarios, we used a thermodynamics-inspired model based on Michaelian (2005) with a genetic algorithm optimisation process (see

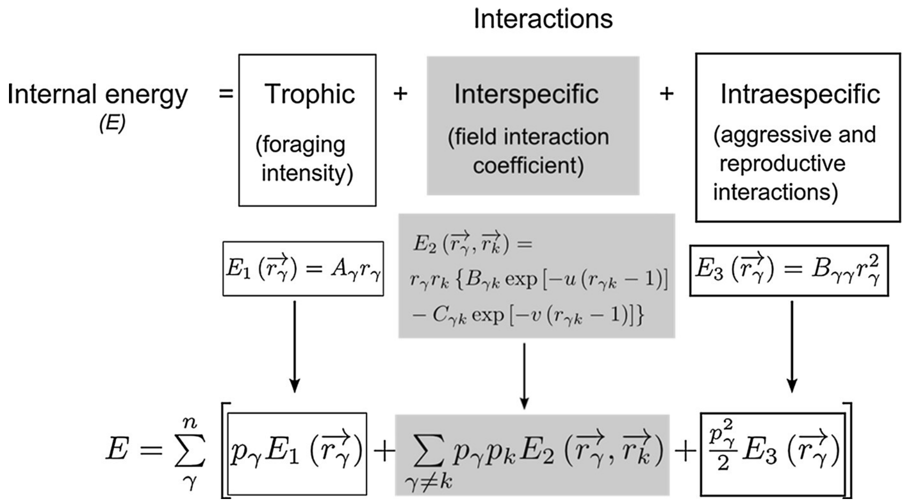

Fig. 2 Thermodynamic model simplified to show how laboratory and field data were incorporated into it; a full description of the model is found in the supplementary materials. E = internal energy; p = population size; E_1 contribution of trophic interactions to E; r = mean food intake; E_2 = contribution of interspecific interactions to E; $B_{\gamma\kappa}$ = competition coefficient for abiotic resources; $C_{\gamma\kappa}$ = competition coefficient for biotic resources; E_3 = contribution of intraspecific interactions to E; $B_{\gamma\gamma}$ = coefficient of intraspecific interactions; A, u and v are normalization constants; γ denotes *G. multiradiatus* and κ denotes *P. bimaculatus*

Michaelian 2005; Chávez and Michaelian 2011for details). This conceptual framework has been successfully applied before to the study of ecological systems (Swenson 1989, 1997; Michaelian 2005; Vallino 2010; Kleidon et al. 2010; Dyke and Kleidon 2010; Chávez and Michaelian 2011). Our thermodynamic analysis assumes that: (1) ecological systems are well described by thermodynamics away from equilibrium; (2) if the individual is regarded as the basic unit of analysis, then the dynamics of the system is well described by using second-order interactions; (3) the system satisfies the 2nd law of thermodynamics; (4) even away from equilibrium, and with environmental conditions dependent on time (extension of Michaelian's work), thermodynamic systems are governed by the principle of maximum entropy production (Swenson 1989, 1997; Vallino 2010; Kleidon et al. 2010; Dyke and Kleidon 2010); and (5) ecological systems tend to stationary states where internal energy (E) is minimized.

The internal energy (E) expressed by equation (1) depends on the population sizes (p) and has three components: the trophic interactions of the species with the environment (E_1), where r_γ is the mean food intake; the interspecific interactions (E_2), where $B_{\gamma\kappa}$ and $C_{\gamma\kappa}$ are competition coefficients for abiotic and biotic resources; and the intraspecific interactions (E_3), where $B_{\gamma\gamma}$ is a intraspecific competition coefficient (Fig. 2; Table 1). These coefficients were derived from our data as follows. From the results obtained in the environmental chambers we took the mean food intake as a measure of foraging intensity (f_γ), and the joint effects of aggressiveness ($a_{\gamma\gamma}$) and reproductive approaches ($c_{\gamma\gamma}$) as a coefficient of intraspecific interactions. From the field data we calculated an interspecific interaction coefficient (i_{12}) that measures the effect of the presence of the exotic species on the native one, and is based on the standardized differences between the abundances of *G. multiradiatus* in Zempoala and in Tonatiahua (*sd*), thus reflecting the long term effect of the coexistence of the native and invasive species (Fig. 2). For simplicity, we standardized all coefficients.

Taking the two extreme conditions (minimization of internal energy and maximization of entropy production) as objective functions, and the corresponding values of coefficients *f*, *a*, *c* and *i*, it is possible to determine the corresponding species' relative abundances using an optimization search procedure of the type known as genetic algorithms (Sastry 2007). To use these results as a predictive tool, a linear model was obtained with R software for the

Table 1 Coefficients used in the thermodynamic model

T(°C)	f1	c11	a11	f2	c22	a22	i12*
10	0.614	0.336	0.008	0.021	0.231	0.006	0.464
14	1	0.573	0.029	0.03	0.44	0.033	0.058
18	0.869	0 433	0.571	0.191	0.752	0.274	-0.348
22	0. 636	0.153	1	0.496	1	0.342	-0.753
26	0.53	0.155	0.822	0.597	0.599	0.547	-1.159

Temperatures were those used in the laboratory to test behavioural performance, whence most of the following coefficients originated: f = feeding performance (mean food intake); c = intraspecific courtship performance; a = negative intraspecific (aggression) interactions; and i = interspecific interaction coefficient (from the field; Fig. 2); for species 1 (*G. multiradiatus*) and 2 (*P. bimaculatus*)

* Calculated from field data

Table 2 Results of two-factor ANCOVAs on behavioural performance profiles obtained in the laboratory

Variables	Factor	Wilks'Lambda	Rao's R	df1	df2	p level
I. Behavioural differences between species						
Feeding responses (latency, foraging frequency)	Temperature	0.893	6.801	8	934	0.000
	Species	0.812	54.139	2	467	0.000
	Both	0.926	4.563	8	934	0.000
Sexual responses (latency, approaches frequency, approaches duration)	Temperature	0.925	6.107	3	226	0.001
	Species	0.839	3.417	12	598	0.000
	Both	0.916	1.675	12	598	0.068
Agressive responses (attacks frequency, attacks duration)	Temperature	0.864	17.867	2	227	0.000
	Species	0.685	11.814	8	454	0.000
	Both	0.908	2.821	8	454	0.005
II. Behavioural differences between populations						
Feeding responses (latency, foraging frequency)	Temperature	0.900	25.890	2	467	0.000
	Species	0.892	6.841	8	934	0.000
	Both	0.939	3.754	8	934	0.000
Sexual responses (latency, approaches frequency, approaches duration)	Temperature	0.737	26.891	3	226	0.000
	Species	0.882	2.415	12	598	0.005
	Both	0.886	2.330	12	598	0.006
Agressive responses (attacks frequency, attacks duration)	Temperature	0.786	30.827	2	227	0.000
	Species	0.650	13.631	8	454	0.000
	Both	0.842	5.080	8	454	0.000

stationary thermodynamic states at the five temperatures used to construct the performance curves. Using the resulting model and the adjusted curves of both the mean-water-depth lake shore temperature, and monthly total fish abundance from the field, we calculated the expected native-invasive population abundances under the different scenarios of climate change proposed by the IPCC (Solomon et al. 2007). As the IPCC scenarios are based on ambient (air) temperature, whereas we are working with mean water shore lake temperature, the scenarios were corrected after calculating the difference between the two temperatures.

For the sake of clarity, a competitive advantage index for *G. multiradiatus* (CAI) was introduced: $CAI = ((RG–RH)/Na)/Rmax$. Where RG is the relative abundance of *G. multiradiatus*; RH is the relative abundance of *P. bimaculatus*; Na is the normalized total abundance of fishes and $Rmax$ the largest value of $RG–RH$ in our sample, divided by Na. In this form,

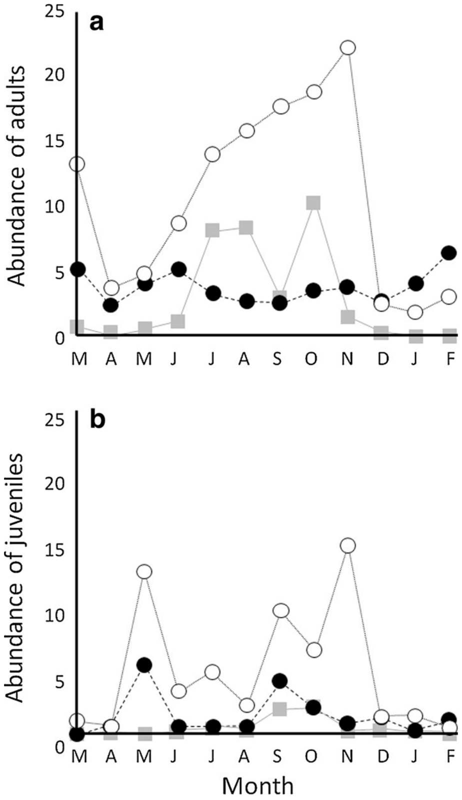

Fig. 3 **a** The standardized abundance (total capture per species per number of sampling points in each lake) of adult *G. multiradiatus* was lower at Zempoala (*closed circles*), than at Tonatiahua (*open circles*) except in the coldest months. The invasive *P. bimaculatus* (*gray squares*) was abundant only in the summer. **b** Negative effect of the presence of *P. bimaculatus* (*gray squares*) on the abundance of juvenile *G. multiradiatus* in Zempoala (*closed circles*) with respect with Tonatiahua juveniles (*open circles*)

when *CAI* = *0* no species predominates over the other; if *CAI* > *0* then *G. multiradiatus* predominates over *P. bimaculatus*; and for *CAI* < *0* the predominant species is *P. bimaculatus.*

Results

Local and temporal variation in fish abundance was a function of temperature. During the cooler months the native species predominated, whereas *P. bimaculatus* was the most abundant in the warmer months (Fig. 3). A population deficit of *G. multiradiatus* in the warmer months was correlated with the presence of the *P. bimaculatus*. This is evidenced by the low numbers of adult *G. multiradiatus* in Zempoala from March to November and their high abundance at Tonatiahua, where *P. bimaculatus* has not been introduced (Fig. 3). This pattern was reversed in the colder months.

The abundance of juvenile *G. multiradiatus* differed markedly between lakes (Fig. 3). Juvenile *G. multiradiatus* remained abundant throughout the year in Tonatiahua, while the peak abundance of juveniles in Zempoala closely followed the recruitment peak of *P. bimaculatus*. There was also an interesting gap between the recruitment peaks of both species. The early peak of *G. multiradiatus* occurred nearly 2 months before the peak of *P. bimaculatus*, which took place in the summer (Fig. 3).

The decision tree resulting from our data mining exercise revealed that temperature was indeed the principal decision variable (first node) to classify each of the 168 samples by species dominance (14 points sampled monthly through a year; accuracy = 50.59 %; Fig. 4. The accuracy is relatively low, probably because of the small sample size for this type of analysis (Kohavi 1996). In particular the *G* classification (only *G. multiradiatus*) had the greatest accuracy. At temperatures ≤14.08 °C the native *G. multiradiatus* (G) invariably dominated, whereas above 21.36 °C the lowland exotic *P. bimaculatus* (H) always predominated. At intermediate temperatures, the micro habitat structure determined which species (if any) dominated, with G > H in sandy substrates, and H > G in areas of rocky substrate. Where the substrate is a mixture of rocks and sand, high dissolved Oxygen and nitrate concentrations also tipped the balance towards *P. bimaculatus* preponderance (H > G).

Laboratory trials at controlled temperatures at which both species survive (10, 14, 18, 22 and 26 °C) showed that the thermal performance profiles of both species and both populations are different for foraging, sexual and aggressive behaviours. Performance profiles of feeding and sexual behaviour of *G. multiradiatus* peaked at lower temperatures (14 °C) than those of *P. bimaculatus*, which either peaked at 22–24 °C, or were open-ended within the thermal interval used here (Fig. 5; Table 2). Interestingly, laboratory maximum performance temperatures were consistent with the field temperatures at places/times when fish of either species were numerically superior (below or above 14 °C), as the decision tree revealed (Fig. 4). The number of approaches of male *P. bimaculatus* towards *G. multiradiatus* females increased with temperature

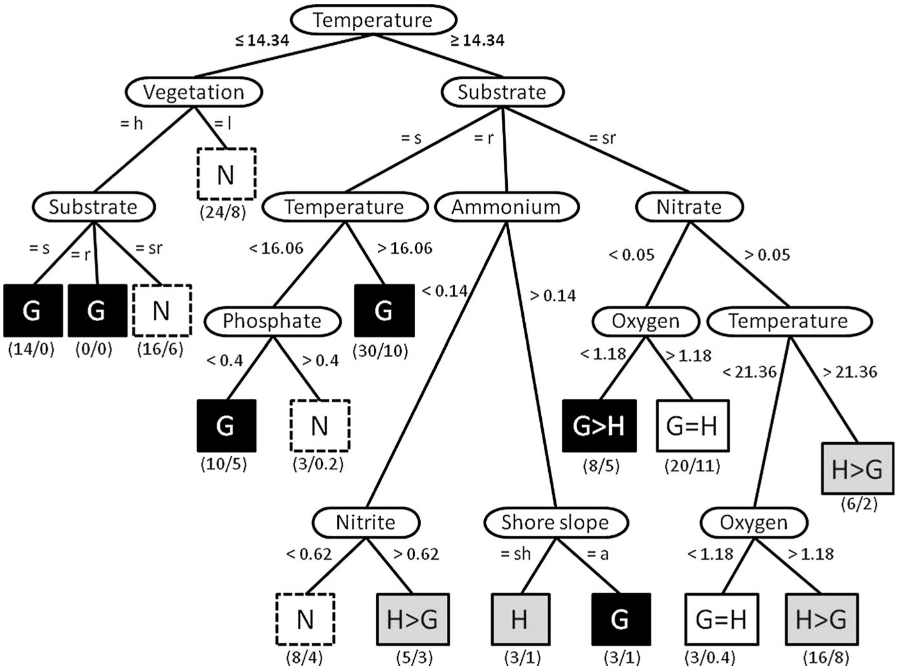

Fig. 4 Decision tree obtained through data mining (see text). Species composition (*black* = *G. multiradiatus* preponderance; *gray* = *P. bimaculatus* preponderance; *white* = either coexistence or absence of both [*dashed blocks*]) is first explained by temperature (°C; initial node), which plays a role at different levels in the tree. Water chemistry, including nutrient concentrations and dissolved oxygen (mg/L), and habitat attributes such as type of substrate (sandy and/or rocky) and location (in shore or away from shore) also explain species composition, with degraded conditions generally favouring the invasive *P. bimaculatus*. The numbers in parentheses below each *box* indicate the bootstrapped ratio of times when samples in each condition (e.g. T °C < 14.34, high vegetation coverage and sandy substrate) were assigned to the correct (=observed) category of fish abundance (e.g. preponderance of *G. multiradiatus*), to the number of times they were assigned an incorrect category of fish abundance (figures >1 rounded to the nearest integer; 0/0 denotes an environmental combination of variables that was not found in our sample but was expected to occur and to harbour a particular fish composition)

(Fig. 5). These were often associated with copulation attempts (not quantified). *G. multiradiatus* from Zempoala were more abundant than the lowland poeciliid during the cold months, and its performance peak occurred at lower temperatures than that of conspecifics from adjacent, poeciliid-free, Tonatiahua (Figs. 3 and 5). Also, its abundance was higher during the coldest months than that of their Tonatiahua counterparts. The standardized difference between the abundance of *G. multiradiatus* in Zempoala and in Tonatiahua (*sd*) can be described as a linear function of temperature ($sd = -0.1\mathrm{T} + 1.47$, $t_{(\mathrm{intercept})} = 2.30$, $p = 0.04$; $t_{(\mathrm{slope})} = -2.64$, $p = 0.02$; $R^2 = 0.41$).

Our thermodynamic linear model takes laboratory data (performance at different temperatures) as inputs, and one coefficient relating the abundance of *G. multiradiatus* in the lakes with- and without the invasive poeciliid (i.e. abundance data from Zempoala are not part of the model). For this thermodynamic analysis we assumed that the ecological system will move towards stationary states where the internal energy is minimized and entropy production is maximized. Our model predicts that under all the scenarios predicted by the IPCC, increases of temperature will result in the decrease of the native species, with the invasive becoming dominant most of the year (Fig. 6). In *status quo* situation, the native species exhibits an advantage over the invasive during most of the year, barring only the warmest month of July, when the situation is reversed. However, even considering the more conservative scenario, *G. multiradiatus* loses its competitive advantage in the breeding months (Fig. 6).

Discussion

One of the most pervasive ecological effects of the current climate warming is the alteration of the timing

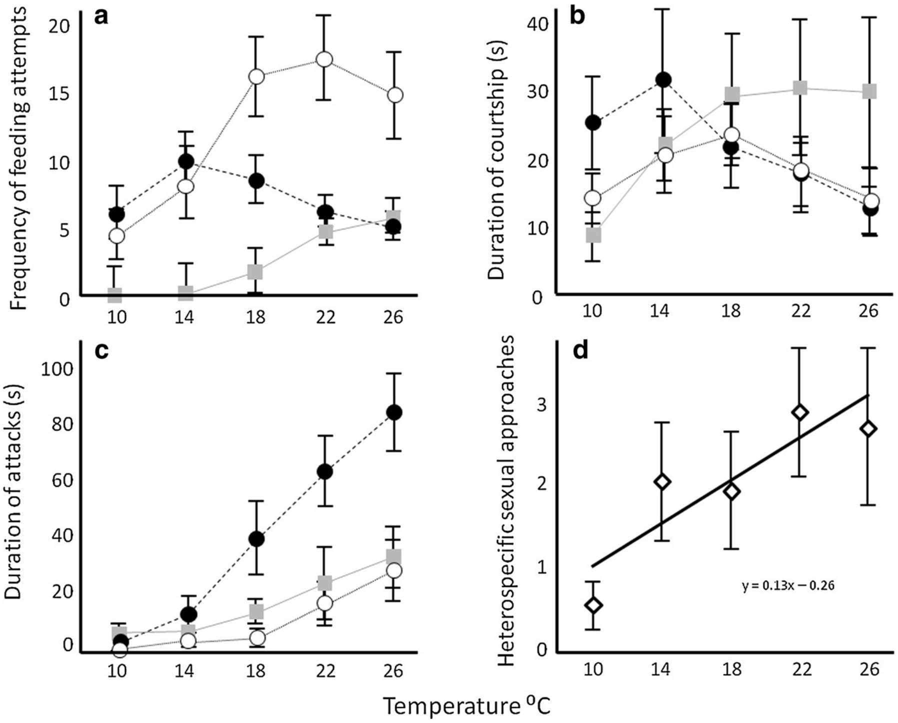

Fig. 5 Feeding (**a**) and courtship performance (**b**) of adult *G. multiradiatus* collected from Zempoala (*closed circles*) was maximal at lower temperatures than that of their conspecifics from Tonatiahua (where the poeciliid has not been introduced; *open circles*) and of *P. bimaculatus* (*gray squares*), which may perform even better at higher temperatures. Aggression (**c**) increased with temperature in all fish, but the raise was steeper for *G. multiradiatus* from Zempoala. The number of approaches (**d**) of male *P. bimaculatus* towards *G. multiradiatus* females increased with temperature (approaches often included gonopodial thrusts; $R^2 = 0.79$; $F = 11.04$, $p = 0.04$; $t_{slope} = 3.32$, $p = 0.04$)

of ecosystem processes. This can induce phenological changes (Parmesan 2006; McEwan et al. 2011; Diamond et al. 2011; Blanchet and Dubut 2012), potentially resulting in large effects on species assemblages (Moussus et al. 2011). A major complication occurs when species simultaneously face the consequences of climatic change and of interactions with invasive species, each promoting opposite phenological shifts. Our data suggest that the differences in phenology between Tonatiahua -presumably the natural condition of *G. multiradiatus* in these mountain lakes- and at Zempoala are linked to the introduction of the invasive *P. bimaculatus* to the latter. In Tonatiahua, *G. multiradiatus* experiences several recruiting peaks throughout the year (except in the colder months) and has two smaller recruiting peaks just before the invasive species' breeding season, one in May and one September. This change in the life history is likely to result in a reduction of interspecific competition faced by the juveniles, and favour surviving climate change as suggested by Blanchet and Dubut (2012). Nevertheless the abundance of adult *G. multiradiatus* in the presence of the invasive poeciliid remained virtually constant through the year, though at considerably lower values than at Tonatiahua. Interestingly, the maximum number of *G. multiradiatus* at Zempoala was found during winter, when it exceeded the abundance of their Tonatiahua counterparts, and which coincided with the decline of the numbers of *P. bimaculatus*. We characterized the shifts in abundance during a single year, yet the proximity of the two lakes and our descriptions of their very similar physicochemical conditions suggest that the differences between the two populations of *G. multiradiatus* are causally linked to the introduction of *P. bimaculatus*. While the actual magnitude of those differences may differ between years, we suspect that our data provide an accurate snapshot of the magnitude and direction of the effects of *P. bimaculatus* on the Zempoala population of *G. multiradiatus*.

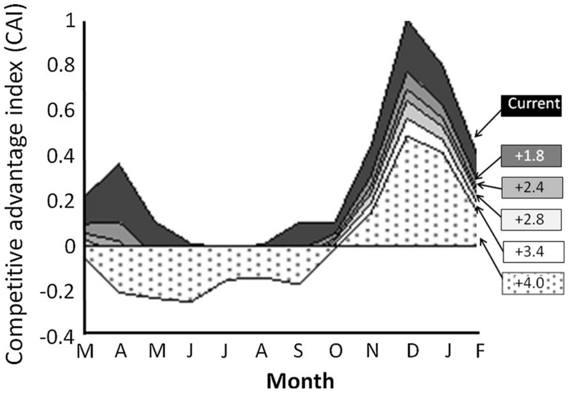

Fig. 6 Demographic projections under different climate warming scenarios. The competitive advantage index (CAI; see Methods) represents the expected relative abundance of *G. multiradiatus* at different temperatures as predicted by a thermodynamic model that incorporates the performance curves of both species, and the demographic deficit of *G. multiradiatus* in Zempoala with respect to the demography at Tonatiahua. Under current conditions *G. multiradiatus* predominates for most of the year (*black polygon*, *positive values*); but increases in temperature promote the competitive advantage of the invasive species (*dashed polygon*, *negative values*); and under scenario A1F1 (+4 °C), *G. multiradiatus* will be competitively superior only during the winter months

In the laboratory, peak performance of *G. multiradiatus* from Zempoala occurred at lower temperatures than that of fish from adjacent Tonatiahua. Since the only major ecological difference between the two lakes is the presence of *P. bimaculatus*, it appears that the difference is due to the selection to reduce the impact of (negative) interactions with the introduced poeciliid, which is least competitive at low temperatures. It thus appears that the response of the native species to the interaction with the invasive exotic has led to displacement of its thermal niche. However, in the absence of data before the introduction of *P. bimaculatus*, we cannot prove this hypothesis. This characters displacement, whether the consequence of natural selection on thermal niche or an expression of phenotypic plasticity, may increasingly confine *G. multiradiatus* to colder periods and micro-habitats. In the face of global climate warming, this confronts *G. multiradiatus* in Zempoala with a seemingly insoluble dilemma, since the cold conditions to which it may be progressively adapting as a consequence of the interaction with *P. bimaculatus* will become increasingly rare, while at the same time climate warming will steadily improve condition for its poeciliid competitor (Walther et al. 2002). Our data may thus lend weight to the warning expressed by Sorte et al. (2010) that climate warming can affect natural communities both via direct impacts on the diversity and abundance of native species, and indirect effects due to increased dominance of the introduced ones. In the view of current climatic trends, this survival dilemma may become commonplace for species in temperate habitats, as competition with invasive tropical/subtropical species would promote thermal niche character displacement towards colder conditions, while global warming would impose an opposite pressure to adapt to warmer circumstances.

Our predictions for all the IPCC scenarios suggest that an increase in temperature will benefit the invader, with the number of months in which it achieves competitive advantage increasing with temperature. This result is similar to the findings of Carmona-Catot et al. (2013) who examined the effects of temperature on competitive interactions between invasive mosquitofish, *Gambusia holbrooki*, and an endemic Iberian toothcarp, *Aphanius iberus*. Our prediction is probably conservative, since an increase in the number of months in which *P. bimaculatus* predominates will probably limit a decreasing population of *G. multiradiatus* to an increasingly impoverished environment in winter. As suggested in Rahel and Olden (2008), new prevention and control strategies such as barrier construction or removal efforts may be needed to control invasive species such as *P. bimaculatus* that currently have only moderate effects or that are limited by seasonally unfavourable conditions.

Because they naturally lend themselves to the incorporation of temperature as an explanatory variable, out-of-equilibrium thermodynamics models like the one developed here may be a useful tool to study species interactions under climatic change scenarios. This conceptual framework proposes that ecological systems evolve to stationary states where the internal energy is minimized and entropy production is maximized.

While the interspecific consequences of phenological shifts have been well documented, their effect on intraspecific interactions and their evolutionary consequences remain relatively unexplored (Heard et al. 2012). Understanding such evolutionary consequences of climate change should be a research priority because of the coupled effects of climate change and competition with exotic species. A further layer of complexity that also needs to be addressed is how changing interspecific relationships contribute to community- and ecosystem-level responses to environmental change (see Harley 2011).

We suggest that the survival dilemma facing *G. multiradiatus* will become commonplace for species in temperate habitats confronted by warming environments. Global warming will increasingly promote competition with invasive tropical/sub-tropical species, leading to thermal niche character displacement towards colder conditions, but at the same time it will create an opposite pressure to adapt to warmer circumstances.

Acknowledgments We are grateful to E. A. Luna for technical support. We thank O. López Corona for his technical assistance with the model and field work, L. Ramírez Carrillo for fish photographs and R. Dirzo for critically reading the manuscript, which was further improved thanks to the suggestions of the associate editor. We are grateful to all the Animal Behaviour laboratory members who helped us in different ways during the project. This paper constitutes a partial fulfilment by ERC of the requirements to obtain a Doctorate under the supervision of CMG within the Posgrado en Ciencias Biológicas of the National Autonomous University of México (UNAM). ERC acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACyT) and UNAM.

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