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Could climate change benefit invasive snakes? Modelling the potential distribution of the California Kingsnake in the Canary Islands

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A B S T R A C T

The interaction between climate change and biological invasions is a global conservation challenge with major consequences for invasive species management. However, our understanding of this interaction has substantial knowledge gaps; this is particularly relevant for invasive snakes on islands because they can be a serious threat to island ecosystems. Here we evaluated the potential influence of climate change on the distribution of invasive snakes on islands, using the invasion of the California kingsnake (*Lampropeltis californiae*) in Gran Canaria. We analysed the potential distribution of *L. californiae* under current and future climatic conditions in the Canary Islands, with the underlying hypothesis that the archipelago might be suitable for the species under these climate scenarios. Our results indicate that the Canary Islands are currently highly suitable for the invasive snake, with increased suitability under the climate change scenarios tested here. This study supports the idea that invasive reptiles represent a substantial threat to near-tropical regions, and builds on previous studies suggesting that the menace of invasive reptiles may persist or even be exacerbated by climate change. We suggest future research should continue to fill the knowledge gap regarding invasive reptiles, in particular snakes, to clarify their potential future impacts on global biodiversity.

1. Introduction

Biological invasions are a pervasive cause of biodiversity loss (Bellard et al., 2016; IPBES, 2018a), but their interaction with other global change drivers represents an even more pressing challenge for conservation worldwide (Bellard et al., 2014; IPBES, 2018b). Climate change in particular is expected to highly influence biological invasion dynamics, modifying introduction pathways and establishment rates of invasive species, fueling their expansion, and increasing their impacts on native ecosystems (Hellmann et al., 2008; Walther et al., 2009; Mainka and Howard, 2010; Huang et al., 2011; Bellard et al., 2018).

However, this response is expected to be highly context-dependent, with some regions of the world being more favorable than others to the invasion of certain taxonomic groups (Bellard et al., 2013; 2018; Li et al., 2016).

Understanding the interaction between invasive species and climate change is particularly challenging on small geographic scales (Bellard et al., 2018). Research addressing this synergy, which is mainly based on species distribution modeling (hereafter SDM), is typically focused on large geographical areas, whereas predictions differ substantially at finer scales (reviewed in Bellard et al., 2018). This is especially true for islands, which despite being an international conservation priority due

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to their extraordinary biodiversity (McGeoch et al., 2016; IUCN, 2018) have been the subject of comparatively little research in this area (Bellard et al., 2018; but see Li et al., 2016). Additionally, SDMs are taxonomically biased, as invasive vertebrates remain largely neglected despite their major role in global biodiversity loss (Bellard et al., 2016; Doherty et al., 2016). This bias is more pronounced for invasive reptiles, for which only a handful of studies exist (Pyron et al., 2008; Rodda et al., 2009; Bellard et al., 2013, 2014; Jarnevich et al., 2018). For invasive snakes in particular, little is known about the way climate change will affect their invasion dynamics on islands (but see Rödder and Lötters, 2010; Silva-Rocha et al., 2015), despite their drastic impacts on native populations and production of cascading extinction events (Kraus, 2015) that potentially lead to major ecological disturbances (Rogers et al., 2017) and far-reaching ecosystem-wide impacts (Caves et al., 2013). Considering that many tropical and subtropical islands are biodiversity hotspots, highly vulnerable to climate change (Bellard et al., 2014), evaluating potential distributions of invasive snakes under climate change is useful as the invasive capacity for some species peaks in these regions (Rodda et al., 2009; Rödder and Lötters, 2010).

With this study, we delve into invasive snakes' response to climate change on islands, using the invasion of the California kingsnake (*Lampropeltis californiae*) as the model. *Lampropeltis californiae* is a colubrid snake, native to and broadly distributed across the Mediterranean climate zone of the southwestern coast of the US and the Peninsula of Baja California in Mexico (Hubbs, 2009; Pyron and Burbrink, 2009). The species is frequently sold as pets in the wildlife trade, but at this time invasive populations are only known in Gran Canaria (Canary Islands) (Monzón-Argüello et al., 2015). The first record of the species in the wild on the island, where no native snakes have ever occurred (García-Talavera et al., 1998), dates back to 1998 (Cabrera-Pérez et al., 2012). Since 2007, the species has steadily increased its invasive range, currently having numerous invasion nuclei, despite the control programs implemented (Cabrera-Pérez et al., 2012; GESPLAN, 2015; www.lifelampropeltis.com). The species chiefly consumes the only three endemic reptiles of the island (Monzón-Argüello et al., 2015), which are crucial elements of the ecosystems (Olesen and Valido, 2003; Nogales et al., 2016; Valido and Olesen, 2019), causing their extinction or drastic reduction (Piquet et al., 2018; Piquet et al. under review). Thus, *L. californiae* is now considered a major conservation problem in the archipelago.

Despite the Canary Islands having numerous mesoclimates due to their orographic complexity (García Herrera et al., 2001; Whittaker and Fernández-Palacios, 2007), the climate broadly mirrors climatic conditions of the species' native range (Beck et al., 2018). Thus, our hypothesis is that a large part of the archipelago will be suitable to the invasive snake both under current and future climatic scenarios. Under this hypothesis, the purpose of this study is two-fold: (1) to assess the potential distribution of *L. californiae* across the Canary Islands under current and future climatic conditions using an SDM approach with the goal of producing information that can inform species management actions and raising awareness, and (2) to increase our general understanding of the interaction between biological invasions and climate change for invasive snakes on islands.

2. Methods

2.1. Native and invasive occurrence data

We extracted occurrence data for the native range by combining data harvested from the Global Biological Information Facility (https://www.gbif.org/), HerpMapper (https://www.herpmapper.org/), herpetofaunal field surveys (see Fisher et al., 2008; Fisher et al., 2019) and other presence data (B. Hinds, unpublished data). We trimmed these datasets to remove invalid records, and re-sampled the resulting 1403 records from the native range to a 0.0083° grid (c. 1 km^2 near the equator) to prevent overlap among datasets and to increase the

performance of subsequent models (Boria et al., 2014) (see Supplementary Information S1 for more details on occurrence data on the native range).

Snake occurrence data in Gran Canaria, corresponding to captured individuals, feces or shed skins (8515 records), was extracted from a public database with all snake presence data collected between April 2009 and December 2019 (www.lifelampropeltis.com). We removed all imprecise geospatial information, divided the island into 0.0083° (c. 1 km^2 near the equator) grid cells (n = 2033), and retained only those grids with established or incipient (recent, small and localized populations) invasive populations to avoid the inclusion of snake records derived from punctual introductions or release of pets (as detected in Monzón-Argüello et al., 2015) —*i.e.*, those not reflecting the true climatic niche of the species (see Supplementary Information S1 for details).

We finally used a total of 988 occurrence grids from the native and 80 grids from invasive range for subsequent analyses.

2.2. Environmental data for current and future climatic scenarios

We downloaded 19 climatic variables from Worldclim (Hijmans et al., 2005) for the native and invasive range at a 0.5 min resolution (c. 1 km^2 near the equator), both for current and future climatic scenarios. For the latter we used two alternative representative concentration pathways (RCP): RCP 2.6 —radiative forcing peaks by 2050— and RCP 8.5 —rising until 2100— (Moss et al., 2010; Meinshausen et al., 2011) (see Supplementary Information S1 for further details on climatic variables). We retrieved elevation at 30-arc seconds resolution (c. 1 km^2 near the equator) using the GTOPO30 digital elevation model from the Earth Resources Observation and Science Center (USGS, 2019).

2.3. Climatic suitability and potential distribution of L. californiae under current climatic conditions

We removed highly correlated environmental variables (Panda et al., 2018; You et al., 2018; Adhikari et al., 2019) using the 'vifcor' function from usdm (Naimi et al., 2014) to prevent multicollinearity and overparameterization (Jiménez-Valverde et al., 2011; Petitpierre et al., 2017). We retained variables with a correlation < 0.7 and a variance inflation factor (VIF) < 5 (Panda et al., 2018). We used selected variables to build four alternative models — BIOCLIM, generalized linear model (GLM), generalized additive model (GAM), and random forest (RF) — and selected a single algorithm with the highest predictive power to evaluate climatic suitability, both in Gran Canaria and in the whole archipelago, following Qiao et al. (2015) (see Supplementary Information S2).

We evaluated climatic suitability for each island using Welch heteroscedastic F tests with trimmed means and Winsorized variances (Welch, 1951) (rate of observations to be trimmed at 0.1), performed in the onewaytest package (Dag et al., 2018). We used the 'paircomp' function for pairwise comparisons among islands, after adjusting confidence levels with Holm's method (Holm, 1979).

To predict the potential distribution of *L. californiae*, we first calculated the favorability threshold for the final selected model that maximized the sum of sensitivity and specificity for each model iteration (maxSSS) (Liu et al., 2013). We used maxSSS, averaged over all model iterations, to transform model projections into binary predictions and characterize favorable and unfavorable areas for the species both in Gran Canaria and in the rest of the archipelago. To measure each climatic variable's contribution to the selected best model, we performed a subsequent analysis following Thuiller et al. (2009) (see Supplementary Information S3). Additionally, to determine the direction of climatic predictors' influence on climatic suitability, we calculated Pearson correlations coefficients between each climatic variable and climatic suitability scores for the best final model.

2.4. Climatic suitability and potential distribution of L. californiae under climate change

Since model predictions are sensitive to the occurrence of novel climatic conditions in projected areas (Elith et al., 2010; Mesgaran et al., 2014), we compared current and future (*i.e.*, averaged over the period 2041–2060) climatic conditions by performing an extrapolation detection analysis in ExDet (Ver 1.1) (Mesgaran et al., 2014). To run this analysis, we used current climatic conditions in the native and invasive ranges pooled together, and climatic predictors from each GCM and RCP in the Canary Islands, separately. By doing so, we aimed to evaluate the existence of Type I (*i.e.*, future climatic conditions falling outside the range of current conditions; *sensu* Mesgaran et al., 2014) and Type II (*i. e.*, variation in the correlation structures for current and future climatic conditions; Mesgaran et al., 2014) ecological novelty. We also evaluated whether future climatic scenarios differed significantly from current climatic conditions in the Canary Islands by comparing them to each RCP scenario with Wilcoxon sign tests.

We obtained future projections of the distribution of *L. californiae* by using ensemble forecasts for each RCP separately; we projected each iteration of the final model for the potential distribution of *L. californiae* to GCM-derived variables, and averaged results for RCP 2.6 and RCP 8.5 separately. We assessed how climate change affected *L. californiae* climatic suitability in the invasive range by calculating for each grid cell the percentage of increase or decrease in climatic suitability from current climatic conditions to each RCP scenario. We then calculated the proportion of grid cells in Gran Canaria alone and the whole Canary Islands presenting climatic suitability increase *vs.* decrease. We also used Wilcoxon sign tests to compare suitability values across the whole archipelago under current and future climatic conditions (RCP 2.6 and RCP 8.5, separately). Finally, we discriminated favorable from non-favorable areas using max*SSS* and evaluated the impact of climate change scenarios on the distribution of *L. californiae* through the species range change (SRC), a parameter commonly used to predict changes in range size (Bellard et al., 2018).

All of these analyses were performed using R 3.5.3 (R Core Team, 2019). For further details, see the accompanying source code (Supplementary Information S4).

3. Results

3.1. Climatic suitability and potential distribution of L. californiae under current climatic conditions

We retained seven climatic layers to represent climatic conditions in the native range and invasive range of *L. californiae* (Supplementary Information S1). The resulting set of climatic predictors presented VIF values below 3 in all cases.

We selected the GLM algorithm as the best model to represent the potential distribution of *L. californiae* in Gran Canaria and the whole Canary Islands (see Supplementary Information S2 for model evaluation metrics), and used the model with proximate non-correlated variables for subsequent analyses (see Supplementary Information S5 for model comparison with orthogonalized variables).

We found that Gran Canaria was climatically extremely suitable for *L. californiae*, as climatic suitability was always above 0.8, with 96.56% of the island having values above 0.9 (Fig. 1). In addition, 98.25% of the Canary Islands had suitability scores above 0.8, with 90.89% of the archipelago over 0.9. Suitability estimates varied significantly among the islands ($F_{6,1811.571} = 460.161$, $P < 0.001$), being higher for Fuerteventura and Lanzarote and lower for La Palma and Tenerife (Fig. 2). Our final model yielded a favorability threshold of 0.468, a value surpassed in all Gran Canaria and most of the archipelago (99.99%) (Fig. 1). Under current climate, higher elevation areas (> 3000 m) were unfavorable (Fig. 1), expressed as different climatic conditions than favorable areas (Table 1). Temperature-related layers were the most important

predictors, with temperature of the driest quarter ($d = 0.137 \pm 0.011$, mean $\pm$ SD) and temperature seasonality ($d = 0.061 \pm 0.006$) being the most relevant. Precipitation of the warmest quarter ($d = 0.008 \pm 0.001$), precipitation of the driest month ($d = 0.007 \pm 0.001$), temperature diurnal range ($d = 0.005 \pm 0.001$), temperature of the wettest quarter ($d = 0.008 \pm 0.001$), and precipitation of the coldest quarter ($d = 0.002 \pm 0.001$) produced lower averaged differences. Climatic suitability was strongly correlated to temperature seasonality ($r = -0.678$; $P < 0.001$), precipitation of the driest month ($r = -0.626$; $P < 0.001$) and temperature of the driest quarter ($r = 0.610$; $P < 0.001$). We found a low correlation between climatic suitability and temperature diurnal range ($r = -0.347$; $P < 0.001$), precipitation of the warmest quarter ($r = -0.209$; $P < 0.001$), precipitation of the coldest quarter ($r = 0.205$; $P < 0.001$), and temperature of the wettest quarter ($r = 0.220$; $P < 0.001$).

### 3.2. Climatic suitability and potential distribution of L. californiae under climate change

We found no Type I or Type II ecological novelty in RCP 2.6 or RCP 8.5, (*i.e.*, the range of values of all ecological conditions and their interactions were similar between current and future climatic scenarios). However, RCP 2.6 and RCP 8.5 scenarios in the whole Canary Islands produced significant differences compared to current climatic conditions for all climatic predictors ($P < 0.001$ in all cases), except for temperature mean diurnal range and precipitation of the driest month (Supplementary Information S6).

Climatic suitability increased in 100% of grid cells of Gran Canaria and the whole Canary Islands, both under RCP 2.6 and RCP 8.5 (Fig. 3), with a total increase of favorable area of 0.01% in the archipelago (measured as a binary variable). A total of 53.80% and 89.40% of Gran Canaria's grid cells increased climatic suitability by more than 0.50% (up to 2.98% and 5.10%) under RCP 2.6 and RCP 8.5, respectively (Fig. 3). RCP 2.6. and RCP 8.5. scenarios increased climatic suitability over 2.00% in 7.80% and 18.00% of the Canary Islands, reaching percentages of increase of 12.23% and 21.33% in high-elevation areas, respectively. Suitability values in the Canary Islands were significantly higher for RCP 2.6 and RCP 8.5 than for current climatic conditions ($P < 0.001$ in all cases) (Fig. 3).

4. Discussion

Although invasive snakes have tremendous impacts on native biodiversity (Kraus, 2015; Rogers et al., 2017) and represent a well-known conservation challenge (Fritts and Rodda, 1998; Rodda et al., 2009; Silva-Rocha et al., 2015), research on their potential distributions is remarkably limited, particularly for islands and under climate change (see Silva-Rocha et al., 2015). In this context, our study presents valuable insights on the potential distribution of an invasive snake in a biodiversity-rich archipelago under current and future climatic conditions. At a regional level, our predictions are contributing to elevate the priority of *L. californiae* management and raise awareness of the value of efficient biosecurity measures across the archipelago.

The Canary Islands are highly suitable for the invasion of *L. californiae*, which adds to previous indications that tropical and subtropical regions are extremely vulnerable to invasion by reptiles in general and snakes in particular (Li et al., 2016). Similar patterns have been found for other snake invasions, such as the invasions of the Burmese python (*Python molurus*) and the brown tree snake (*Boiga irregularis*), whose abilities to invade increase towards the equator (Pyron et al., 2008; Rodda et al., 2009; Rödder and Lötters, 2010). Considering that most biodiversity-rich regions are tropical and subtropical (Myers et al., 2000), these findings underline the significant threat posed by invasive snakes to global biodiversity, especially since these areas are highly susceptible to climate change (Trisos et al., 2020), which increases their suitability to invasive snakes (Rodda et al., 2009; Rödder and Lötters, 2010; Silva-Rocha et al., 2015). Based on that, predicting
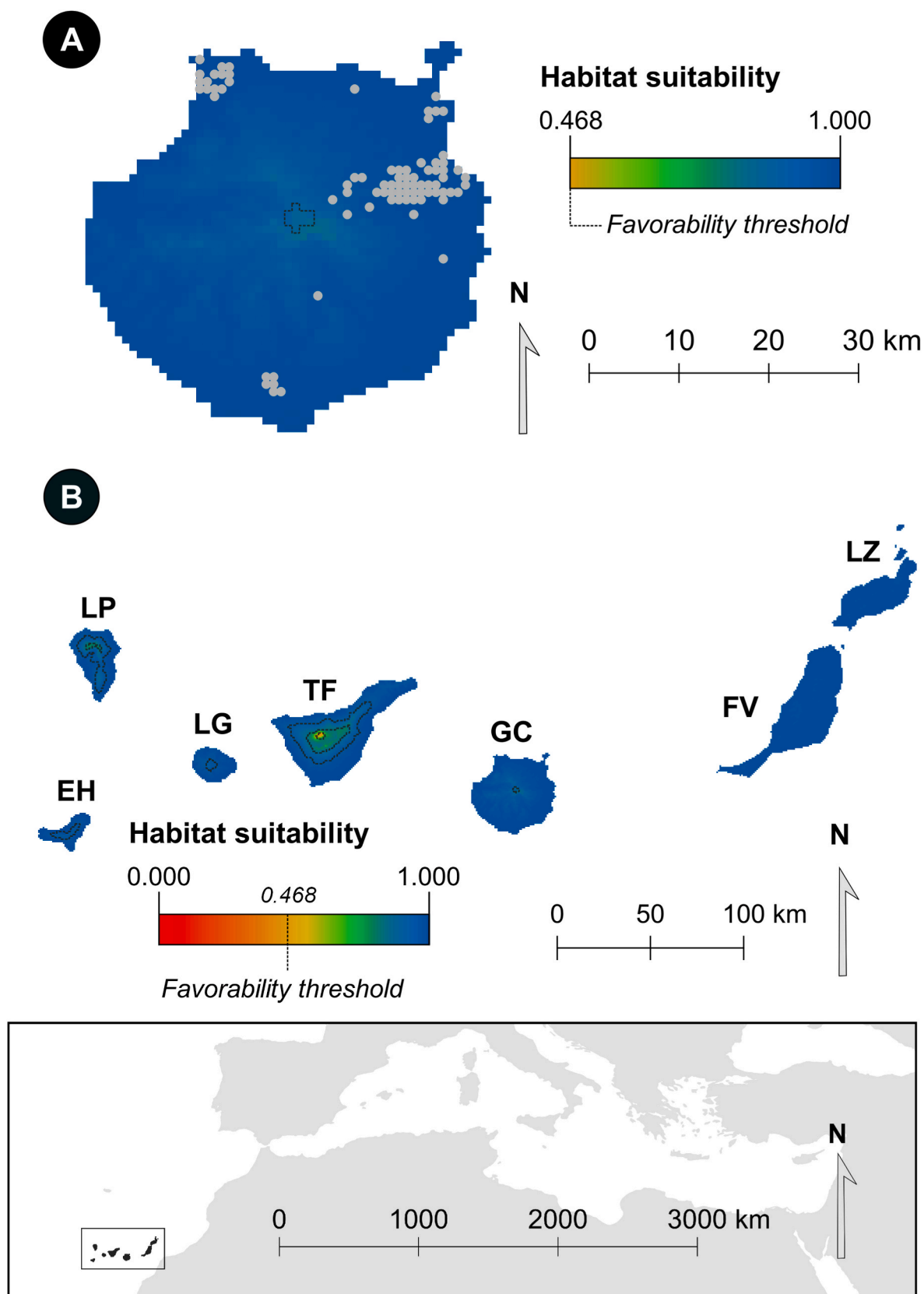
Fig. 1. Projection of the potential distribution of *Lampropeltis californiae* under current environmental conditions in Gran Canaria (A), and the whole Canary Islands (B). Grey dots in A represent presence data in the invasive range (*i.e.*, established populations in the island, derived from snake records including captures, skin sheddings and feces collected between 2009 and 2019). In panel B, La Palma, El Hierro, La Gomera, Tenerife, Gran Canaria, Fuerteventura and Lanzarote, are labelled as LP, EH, LG, TF, GC, FV, LZ, respectively. Contour lines indicate 1000, 2000 and 3000 m of elevation a.s.l.
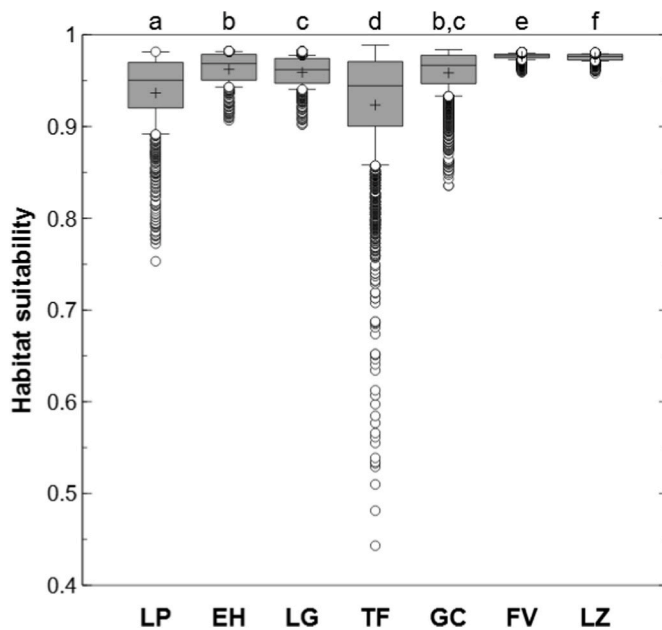
Fig. 2. Average suitability scores per island. LP, EH, LG, TF, GC, FV, LZ correspond to La Palma, El Hierro, La Gomera, Tenerife, Gran Canaria, Fuerteventura and Lanzarote, respectively. Results are presented as mean (+) and SD (error bars). Different letters represent significant ($P < 0.05$) differences in similarity values among islands.

Table 1

Climatic conditions in favorable (suitability scores > 0.468) and unfavorable areas to *Lampropeltis californiae* in the Canary Islands. Values for favorable areas are shown as mean ± SD and range [min, max]. For unfavorable areas, climatic conditions are shown as the value from the single unfavorable grid cell found in the archipelago. Temperature–related variables derive from temperature data measured in °C x 10 (Hijmans et al., 2005), except for temperature diurnal range, mean temperature of the wettest quarter and mean temperature of the driest quarter, expressed as °C. Precipitation variables are measured in mm (Hijmans et al., 2005).

Variable	Favorable	Unfavorable
Temperature mean diurnal range	**7.12 ± 0.30 [6.50, 8.10]**	**8.20**
Temperature seasonality	**2804.22 ± 471.32 [2089.00, 4853.00]**	**4850.00**
Mean temperature wettest quarter	**15.21 ± 3.13 [-0.40, 19.50]**	**−0.90**
Mean temperature driest quarter	**20.76 ± 1.91 [10.80, 24.10]**	**10.40**
Precipitation driest month	**0.49 ± 0.62 [0.00, 3.00]**	**2.00**
Precipitation warmest quarter	**9.19 ± 5.13 [3.00, 32.00]**	**34.00**
Precipitation coldest quarter	**135.01 ± 66.12 [50.00, 294.00]**	**297.00**

the distribution of invasive snakes is valuable for regions near the tropics, which are threatened by their presence or potential introductions (*e.g.*, Fritts, 1993; Fritts and Rodda, 1998; Martínez-Morales and Cuarón, 1999; Quick et al., 2005; Worthington-Hill et al., 2014).

Warm and stable temperatures were found to be the most important climatic suitability drivers for *L. californiae*, which is consistent with variables explaining reptile distributions (Aragón et al., 2010; McCain, 2010; Qian, 2010) and their establishment and spread into novel areas (Mazzotti et al., 2011; Dawson et al., 2017; Lin et al., 2019), usually reflecting their thermal preferences (Rodda et al., 2009; Rödder and Lötters, 2010). For instance, cold intolerance restricts the distribution of the invasive *P. molurus* (Jacobson et al., 2012), and cold winter temperatures prevent elevational expansion of the invasion of many-lined sun skinks (*Eutropis multifasciata*) (Lin et al., 2019). The general importance of temperature on understanding reptile distributions is

especially relevant in the context of invasion biology and future global warming (IPCC, 2013; Li et al., 2016; Trisos et al., 2020). Global warming may lead to more favorable conditions for invasive reptiles, fueling their expansion to novel areas (Rodda et al., 2009; Silva-Rocha et al., 2015) and augmenting their fitness and impacts in ecosystems already invaded (Hellmann et al., 2008; Mazzotti et al., 2011). Climate change may also lead to increasing temperatures and unstable climatic conditions (IPCC, 2013), which could impair invasive reptiles' expansion and success (Mazzotti et al., 2011; Winter et al., 2016). In both cases, physiological tolerance and phenotypic plasticity may play a prominent role in shaping the response of invasive reptiles to changing climatic conditions (Urban et al., 2014; Card et al., 2018). Therefore, to improve the accuracy of forecasts for invasive reptiles, physiological tolerance and adaptive capacity information should be incorporated (Lennox et al., 2015; Beever et al., 2016).

We found that the Canary Islands are expected to become increasingly suitable to *L. californiae*, particularly in high-elevation areas, as a consequence of global warming, leading to its range expansion and coinciding with most SDMs for invasive reptiles (Rodda et al., 2009; Rödder and Lötters, 2010; Silva-Rocha et al., 2015). Most invasive taxa in subtropical areas are expected to undergo substantial range contractions under future climate (Pyron et al., 2008; Bellard et al., 2013; Taylor and Kumar, 2014), although the contractions are expected to be moderate in low latitudes for invasive reptiles, and therefore, often may translate into sustained persistence in tropical and subtropical regions (Pyron et al., 2008; Rödder et al., 2008; Bellard et al., 2013). This is particularly alarming in the case of invasive snakes due to the threats posed by these organisms on the biodiversity of subtropical islands. In this context, additional research to understand their future response to climate change will be valuable, particularly to anticipate their future impacts on biodiversity.

4.1. Management implications for L. californiae

From the species management perspective, as part of a recently-strengthened research program on *L. californiae* management and impacts, this study has triggered the approval of the Strategic Plan for the Control of the California kingsnake in the Canary Islands 2019–2022, which has notably strengthened the investment since the LIFE10 NAT/ ES/000565 Lampropeltis program has ended. Our predictions on climatic suitability and climate change under these two climate scenarios also support the implementation of efficient measures to prevent the species introduction to other islands, particularly given the current lack of biosecurity protocols in the archipelago (*e.g.*, Medina et al., 2018). At a broader scale, Gran Canaria is a hub of tourism and commercial activity within the archipelago (see Medina et al., 2018), the Macaronesian archipelagos, and between Africa, Asia and Europe (Puertos de las Palmas, 2020). Consequently, *L. californiae* poses a serious risk not only for the archipelago, but also to numerous regions well connected to Gran Canaria.

5. Conclusions

The subtropical archipelago of the Canary Islands offers highly suitable conditions for the invasive snake *L. californiae* and the species' potential distribution is expected to increase further under future climate change scenarios, unless effective measures are implemented to control the currently expanding range on Gran Canaria and avoid the invasion of the rest of the archipelago. Our results are consistent with previous research showing that tropical and subtropical areas are vulnerable to invasive reptiles (Rödder et al., 2008; Rodda et al., 2009; Rödder and Lötters, 2010) and support the idea that general patterns for invasive species may not apply to all invasive reptiles. We suggest future research to find efficient methods to control invasive snakes and to continue bridging the current knowledge gap regarding invasive reptiles in order to anticipate their future impacts on global biodiversity.
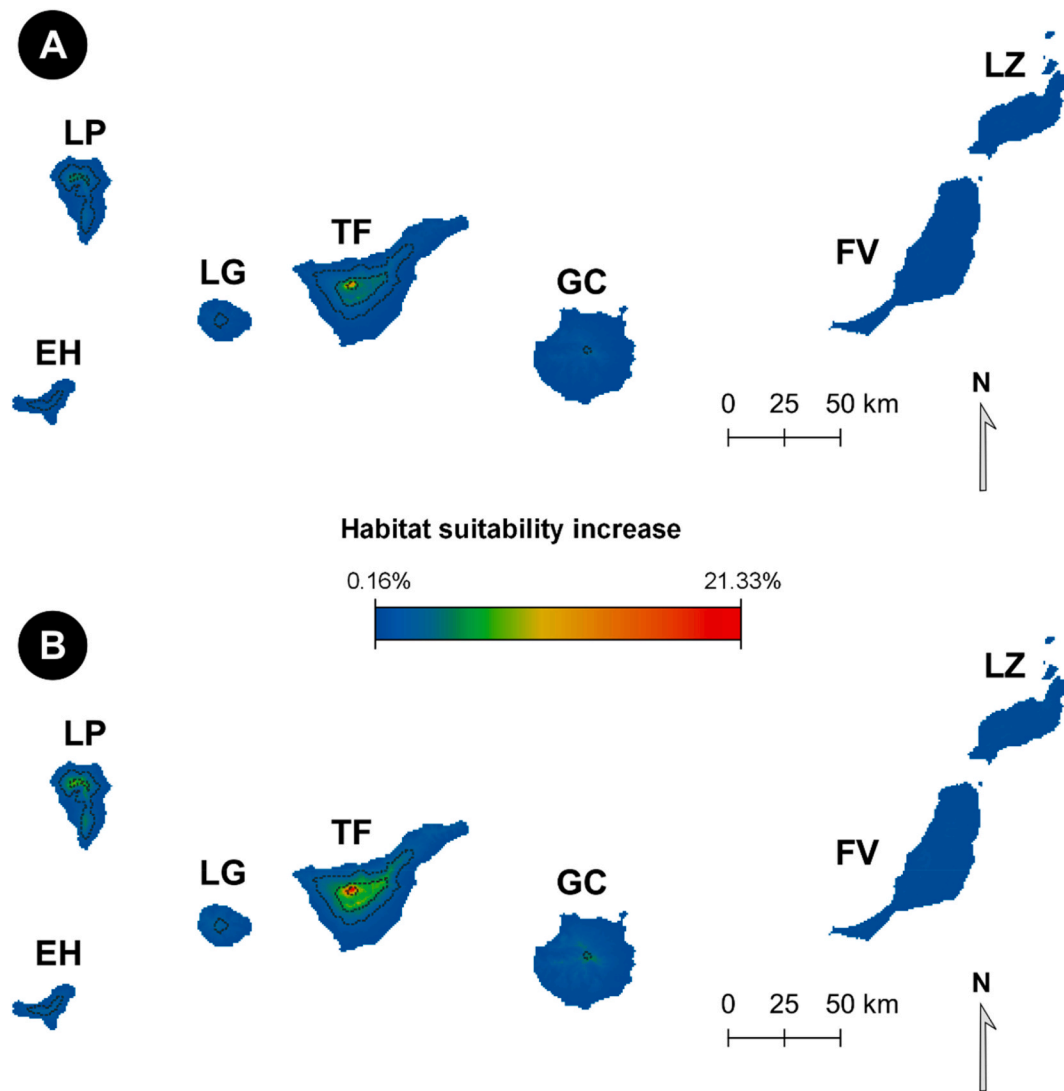
Fig. 3. Climatic suitability increment in the Canary Islands under RCP 2.6 (A) and RCP 8.5 (B). Grid cell values represent the percent increase from current climatic conditions to each of the future climatic scenarios. Contour lines indicate 1000, 2000 and 3000 m of elevation a.s.l.

Credit author statement

Julien C. Piquet: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. Dan L. Warren: Software, Formal analysis, Writing – review & editing, Supervision. Jorge Fernando Saavedra Bolaños: Resources. José Miguel Sánchez Rivero: Resources. Ramón Gallo-Barneto: Resources. Miguel Ángel Cabrera-Pérez: Resources. Robert N. Fisher: Resources, Writing – review & editing. Sam R. Fisher: Resources, Writing – review & editing. Carlton J. Rochester: Resources, Writing – review & editing. Brian Hinds: Resources. Manuel Nogales: Writing – review & editing. Marta López-Darias: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.112917.

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