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Research article

TITLE

Where does the rainbow end? A case study of self-sustaining rainbow trout *Oncorhynchus mykiss* populations in tropical rivers

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ABSTRACT

The great physiological, behavioral and morphological plasticity of salmonids contributed to the success of their introduction into a wide range of habitats. However, rainbow trout (*Oncorhynchus mykiss*) is the only salmonid species to live in the tropics. Like for any cold-water species, water temperature is assumed to be a major constraint to the presence and expansion of rainbow trout. In this study, we investigated key drivers of the establishment of self-sustaining populations of rainbow trout in the tropical rivers of Reunion Island (West Indian Ocean). We collected detailed records of the introduction history of rainbow trout at 38 sites across the island over 80 years to determine whether the presence/absence of trout could be related to the introduction effort. Surprisingly, the presence of trout was limited to 10 known sites and seemed independent of the introduction effort. There was no evidence of large-scale expansion of trout away from introduction sites, and the risk of expansion from current self-sustaining populations appeared low. We then quantified how seasonal water temperatures influenced the presence of self-sustaining populations of rainbow trout. As expected, low temperature is a prerequisite for the presence of trout, which is favored at high elevations in this tropical region. We provide evidence that the presence of trout is limited by temperature in summer and winter, which makes it vulnerable to global warming throughout its life cycle. By translating threshold temperatures into elevation, we estimated the probability of the presence of trout, spatially, after introduction along all perennial rivers of the island. Upscaling results from a few study sites to a larger spatial scale is a useful tool for managers in this and other data-poor areas.

KEYWORDS

Elevation, introduction, presence, salmonid, temperature

DECLARATIONS

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Conflict of interest

The authors declare no conflict of interest.

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INTRODUCTION

Native to the northern hemisphere, salmonid species have been introduced worldwide (Welcomme 1988; Crawford & Muir 2008; Lecomte *et al.* 2013), especially brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*). Their great physiological, behavioral and morphological plasticity contributes to the success of their introduction into a wide range of environmental conditions (Sauter *et al.* 2001). Since they are a cold-water species, however, successful introductions have been reported mainly at high latitudes and in temperate regions (Cowx 1997; Stanković *et al.* 2015; Koutsikos *et al.* 2019), since water temperature is a major constraint to their ontogeny and expansion. Among salmonids, rainbow trout has the widest latitudinal distribution in its native range (Fig. 1a), from 23-64°N (MacCrimmon 1971; Welcomme 1988; Crawford & Muir 2008). The population in the Sierra Madre Occidental Mountains of Mexico represents the southernmost native range of any salmonid (Behnke 2010), along with the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) in Asia. These populations reflect rainbow trout's ability to survive under extreme thermal conditions (MacCrimmon 1971; Gall & Crandell 1992). Its optimal range is 10-16°C, but adults can endure peaks of 25°C (Raleigh 1984; Jalabert & Fostier 2010) and even up to 28-30°C (Matthews & Berg 1997; Sloat & Osterback 2013). In contrast, it reproduces in winter to meet requirements for lower temperatures. Spawning and successful egg development have been recorded at temperatures of 4-13°C (Morrison & Smith 1986; Pankhurst *et al.* 1996; Jalabert & Fostier 2010) and even up to 15.5°C (Scott & Crossman 1973). Above 20°C, however, the fecundity rate and embryonic survival decrease greatly (King *et al.* 2003).

Since the middle of the 20th century, rainbow trout has been massively introduced worldwide for aquaculture and recreational purposes (Welcomme 1988). According to the FAO (2003), at least 97 countries have introduced it (Fig. 1a), including 38 in the tropics (Table S1). To our knowledge, rainbow trout is the only salmonid species that lives in the tropics. Lethal temperature is the main reason that introductions have failed in Puerto Rico, the Philippines, Trinidad and Mauritius (MacCrimmon 1971). Nevertheless, the existence of self-sustaining populations (i.e. recruitment unsupported by and independent of continued human interactions, *sensu* Copp *et al.* (2005)) has been reported in nearly 70% of tropical countries where the species was introduced (Fig. 1b, Table S1). Tropical populations of rainbow trout are presumably found at high elevations, where the ambient temperature is cool (Therezien 1960; Péfaur & Sierra 1998; Ngugi & Green 2007; Vila *et al.* 2007; Kadye *et al.* 2013; Vimos *et al.* 2015), such as in the Nyanga Mountains (>1,800 m) in Zimbabwe or Lake Titicaca (3,812 m) in Peru and Bolivia. However, the dual influence of water temperature and elevation on the success of introduced rainbow

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trout in the tropics has not been clearly determined. In the current context of global warming, understanding how rainbow trout populations respond to high temperatures in tropical regions may help better predict the future of salmonids in their native ranges.

The objective of this study was to investigate how summer and winter water temperatures influence the presence of self-sustaining populations of rainbow trout in tropical regions. After reviewing the literature on tropical populations of the species, we focused on the unique case study of Reunion Island (West Indian Ocean), where rainbow trout has been repeatedly introduced since 1940, with varying success. A dense network of rivers that flow from high-elevation volcanic mountains provides a large gradient of water temperatures. Since early life stages of salmonid species are particularly sensitive to high temperatures (Sullivan *et al.* 2000; Benjamin *et al.* 2013), we explored the influence of winter temperatures as the main driver of successful population establishment after introduction, as well as the possible limiting effect of high summer temperatures. Warming summer temperatures are identified as a main threat for the viability of rainbow trout populations in its native range in the northwestern United States (Sloat & Osterback 2013; Brewitt & Danner 2014). In the tropics, where summer temperatures are already high, warming winters could reach a critical level that is incompatible with trout reproduction and thus become relatively more limiting than in a temperate climate. Our objectives were threefold. We first reviewed and collected the stocking history of rainbow trout on Reunion Island to determine whether the introduction effort influenced the presence/absence of trout. We then used river-specific water temperature records to model the influence of mean monthly temperatures during winter and summer on the successful establishment of rainbow trout populations. Finally, we predicted the probability of the presence of rainbow trout as a function of elevation to provide guidelines for managing rainbow trout populations in the multiple and contrasting landscapes on Reunion Island.

MATERIALS & METHODS

Study site

Reunion Island is a 2,512 km² French overseas department located in the Indian Ocean (21.2°S, 55.6°E). The highest peak of this volcanic island reaches 3,069 m above sea level. Its hydrology is characterized by heavy rain during the cyclone season (December to April). The topography and aquifers generate high spatial and temporal heterogeneity in the quantity of water in rivers (Robert 1985). The island is drained by 13 perennial rivers and 43

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transient watersheds characterized by their high degree of natural habitat fragmentation and their torrentiality, which can reach up to 30,000 l/s/km² on a few km² of watershed (Robert 1985). Anthropogenic barriers, which are less common than natural fragmentation, are restricted mainly to lowland areas.

The rivers of Reunion Island host 26 fish and 11 decapod crustacean species, of which 20 and 10, respectively, are indigenous catadromous species (Keith 2002). Of the seven species that were introduced to the island, only four established self-sustaining populations: tilapia (*Oreochromis niloticus*), guppy (*Poecilia reticulata*), swordtail (*Xiphophorus hellerii*) and the non-anadromous form of rainbow trout (Keith 2002). The presence of juvenile rainbow trout in the absence of introduction, which indicates wild reproduction, is the criterion used to define a self-sustaining population. The presence of self-sustaining rainbow trout populations is assessed by visual observation (e.g. presence of juveniles, acts of spawning, redds) and electrofishing surveys conducted by the local association for fishing and the protection of aquatic environments (hereafter, fishing association). The presence or absence of a self-sustaining population from 2016-2020 was assessed at each site where trout had been introduced, all sites where its presence was suspected, and at all sites where temperature data were available (see below). A site, the smallest spatial unit considered, was defined as a stretch of river a few hundred m long with homogeneous habitat that is usually delineated by natural discontinuities (waterfalls). We assumed that each site's characteristics and dynamics did not change over the five years of the study. Each site was described by a unique identification number, the river and local name, elevation (Table S2) and geographic coordinates (Fig. S3).

Introduction history of rainbow trout

The rainbow trout introduced to Reunion Island have come from Madagascar (Robert, 1975), with the initial objective to provide a new source of food for the French colony (Robert, 1978). To understand how introduction effort influences the presence of trout, we reviewed the available reports to update the history of trout stocking on Reunion Island. The main sources of information were publications by R. Robert (Robert 1975, 1976, 1977, 1978) and reports by the National Forest Office and the fishing association. Despite our efforts to identify all introduction events from 1940-2019, some information from 1940-1950 and 1978-1990 may have been missing due to the loss of archival records. Details about the number of introduction events, the number of trout introduced, the period of introduction and the organization in charge of the introduction were collected (Table S2).

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Temperature data

We investigated the influence of water temperature on the presence of self-sustaining rainbow trout populations on Reunion Island for 33 study sites spread across a wide range of elevations (5-1,470 m). At each site, water temperature was recorded daily from 2010-2021 by autonomous data loggers or fixed meteorological stations (Table S2). The local water agency (http://www.naiades.eaufrance.fr) and the fishing association provided the water temperature data. Mean monthly temperature at 12 p.m. was used as an explanatory variable in the analysis.

Identifying drivers of the presence of trout

We modeled the probability of trout establishing a self-sustaining population as a function of the introduction history. The presence or absence of a self-sustaining population at the time of the study (2016-2020) at each site where trout had been introduced was used as the response variable in a generalized linear model (GLM) with a binomial distribution of errors (Bolker *et al.* 2009). We hypothesized that self-sustaining populations were positively related to the number of introduction events and the number of trout introduced. For some events, reports only tracked the total weight of trout introduced. In the absence of information on the size or weight of trout, we were not able to assess the number of trout considered, thus the recorded number of trout introduced is an underestimation of the introduction effort. We hypothesized that self-sustaining populations were negatively related to the number of years since the last introduction, since the probability that extreme environmental conditions (e.g. cyclonic floods) could extirpate the population increases over time. In addition, the organizations in charge of introductions used trout broodstock from multiple strains and fish farms. Since genetic characteristics and rearing conditions may influence the adaptive capacity of trout introduced into the wild (Araki *et al.* 2008), we included the organization in charge of the introduction as an explanatory factor in the GLM. The effects were selected based on Akaike's information criterion (AIC, Burnham *et al.* 2011). As a measure of how well the model fit the data, we used the deviance-based pseudo-R^2, calculated as (null deviance–residual deviance)/null deviance.

Similarly, we modeled the probability of the presence of trout as a function of mean monthly water temperature and season (the explanatory variables), using a GLM with a binomial distribution of errors. Season was a two-level factor that distinguished the winter "spawning" season (May to September) from the summer "growing" season (October to April). We tested for both additive and interaction effects of temperature and season. Effects were selected based on AIC, and model fit was assessed using the pseudo-R^2. The model with the lowest AIC was selected (hereafter Mtemp).

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Relating temperature to elevation

Autonomous temperature loggers provided detailed measurements of water temperature at the study sites. However, temporal and spatial coverage was often limited by the loss of loggers due to cyclones or vandalism, by the cost of the devices or by the logistical difficulties involved in deploying scientific equipment in a remote area. Thus, our results needed to be upscaled from a few study sites to a large area that is more relevant for conservation. Since temperature depends on elevation, we built a simple GLM to predict the probability of the presence of rainbow trout in all perennial rivers on Reunion Island as a function of elevation. We first explored the linear relationship between mean monthly water temperature and season/elevation using a GLM with a normal distribution of errors. The model was based on temperature and elevation data from all 33 sites (Table S2). From this model, we estimated mean summer and winter water temperatures for 2297 locations along all of the perennial rivers. The elevation of each location was extracted from a detailed topographic map provided by the French digital elevation model (BD ALTI, 25 m resolution, https://geoservices.ign.fr/bdalti). We then calculated and mapped the predicted probability of the presence of rainbow trout at all locations, based on its seasonal temperature preferences as described in the Mtemp model. All analyses were performed using R v4.0.5 (R Development Core Team 2018). Maps were produced using QGis version 2.8.93.10 (https://www.qgis.org/en/site/).

RESULTS

Introduction history of rainbow trout

We found evidence that rainbow trout were introduced into 7 rivers (i.e. Mât, Roches, Marsouins, Galets, Langevin, Remparts and St-Etienne) out of the 13 perennial rivers on Reunion Island (Fig. 2). Historical records documented that 422,905 individuals and an additional 860 kg of rainbow trout were released at 38 sites in these rivers or their tributaries from 1940-2019 (Table S2). The introduction effort varied greatly among sites (Fig. 2), with a single introduction of 200 trout in 2007 at site 44, but 72,325 trout introduced over more than 30 events at site 29. The presence of a self-sustaining population of trout was recorded at 9 sites of the 33 introduction sites whose location was specified (Table S2). We found only one site with a self-sustaining population of trout where no introduction had been documented (site 18). Nevertheless, we observed that trout had been introduced ca. 500 m upstream of this site, at sites 21 and 42. The mean probability of observing a self-sustaining population of trout at one of the 33 sites where trout had been introduced was 0.24 (standard error = 0.075). None of the variables

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tested improved the fit of the constant model, which indicated that trout presence was independent of the introduction effort (Table 1).

Seasonal water temperature profiles

Mean monthly water temperatures at the study sites ranged greatly, from 11.0-22.1°C in winter and 14.6-27.7°C in summer (Fig. 3). Seasonality, which can be described by a decrease in temperature in winter, was distinct at some sites, while temperature profiles remained flat throughout the year at several other sites. Self-sustaining populations of trout were present at sites with low water temperature and high seasonal variability, but some sites with low water temperature had no trout, despite trout introduction. At sites where trout were present, mean temperature in summer and winter were 17.5°C (standard deviation (SD) = 0.8) and 14.9°C (SD = 1.0), respectively. The warmest month on record at a site with trout reached a mean temperature of 19.6°C (SD = 1.04) (site 42 in March 2020).

Water temperatures and the probability of the presence of trout

As expected, the presence of self-sustaining populations of rainbow trout depended greatly on water temperature. However, it also depended on the season, since temperature requirements may vary over the trout life cycle (Table 2). Notably, rainbow trout tolerated higher temperatures in summer than in winter (Fig. 4). The selection of an interaction between temperature and season in the best Mtemp model (Table 2) indicated that trout responded more strongly to an increase in temperature in summer than in winter. The Mtemp model predicted that the probability of the presence of a self-sustaining trout population is less than 0.05 when the mean monthly water temperature exceeds 20.1°C in winter and 20.5°C in summer (Fig. 4). This probability increases to 0.50 when mean water temperature is less than 15.6°C in winter and 18.4°C in summer, and reaches 0.95 when it is less than 11.0°C in winter and 16.4°C in summer.

Contrasting summer and winter water temperatures across sites

The mean monthly water temperatures in summer and winter differed greatly among study sites (Fig. 5) and often exceeded those compatible with a 0.05-0.95 probability of presence of self-sustaining trout populations. At some sites, water temperatures fell within the 0.05-0.95 probability of presence of trout in one season (winter at site 14),

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but not the other season, which compromises the persistence of trout in the wild. At sites 11 and 13, both winter and summer water temperatures were higher than the threshold temperatures needed for a 0.50 probability of presence, which indicated that the presence of trout remained uncertain. However, no trout were observed at these sites. At site 21, winter water temperatures were compatible with a probability of presence greater than 0.50, but summer water temperatures appeared limiting, as confirmed by the absence of trout at this site. At site 20, we observed no evidence that temperatures would limit the presence of trout, although trout were absent.

Using elevation as a proxy of temperature to predict the probability of the presence of trout

Mean monthly water temperature correlated strongly with both elevation and season (Table 3), which explained as much as 76.6% of the variance in the data. Adding the interaction between elevation and season did not improve the fit of the model, which indicated that the mean decrease in water temperature for each m in elevation was similar in winter and summer (Table 3, Fig. 6). However, due to the interaction between temperature and season in the Mtemp model (Table 2), the season that limits the presence of trout may differ among sites with different elevations (Fig. 6). When considering threshold temperatures for a given probability of the presence of trout, the maximum suitable temperature for summer and winter were not reached at the same elevation. For instance, the threshold temperature for a 0.50 probability of presence of trout in winter and summer was predicted to occur at 852 and 872 m, respectively. In this case, mean summer water temperatures were slightly more restrictive for the presence of trout at a given elevation. In lowlands, high temperatures strongly limited the presence of self-sustaining populations, but in highlands, temperatures were more suitable for trout, with a predicted 0.95 probability of presence at 1,782 m and higher. However, the increasing gap between summer and winter requirements with increasing elevation (Fig. 4) indicated that winter was the main driver of trout self-sustainability. To illustrate these results, we developed a map that summarizes the estimated probability of the presence of trout after introduction as a function of elevation for the entire island (Fig. 7).

DISCUSSION

Rainbow trout is a stenotherm species that is native to temperate rivers of North America. It has been extensively introduced all over the world and the literature review indicates that tropical regions are no exception (Fig. 1 and S1). Despite the recognized plasticity of trout, its long-term persistence in the tropics seems challenging due to its affinity for cold water. On Reunion Island, the introduction of trout into at least 38 different sites in river stretches across the country illustrates a long-term and widely spread introduction effort across high-elevation perennial

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248 rivers. Despite the recorded release of > 400,000 rainbow trout, we are aware of only 10 self-sustaining
249 populations. Interestingly, introduction effort had no influence on the presence of self-sustaining populations of
250 trout (2016-2020). Similarly, a review of rainbow trout introduction into the wild in Europe (Stanković *et al.* 2015)
251 reported that self-sustaining populations are rare and unevenly distributed despite its intensive 120-year-long
252 history. This result challenges the relevance and objective of current management practices. Indeed, recent
253 management of trout fishing can be described as 'put and take', with no clear attempt to establish new populations.
254 The fishing association introduces trout at sites chosen for their fishing attributes (e.g. accessibility, scenery),
255 which could be sub-optimal for trout development. The environmental conditions that fish encounter at release
256 sites, however, appear to have a distinct influence on the success of introduction.
257
258 We found no clear evidence of the presence of self-sustaining populations outside sites where trout had been
259 introduced, except for site 18 (Fig. 2), whose immigrants likely originated from the nearby sites 21 and 42, located
260 less than 500 m away. If trout disperse, they likely do so over very short distances. Several environmental factors
261 can hinder trout expansion across rivers on Reunion Island. First, the island's topography, with steep mountains
262 and many natural waterfalls that result in a high level of habitat fragmentation, strongly limits rainbow trout
263 dispersal from introduction sites. Temporary drying of river stretches due to the highly permeable substrate also
264 limits dispersal. We do not know when the populations established, but based on the long history of introduction
265 (> 80 years), it is likely that some populations have sustained themselves for more than one decade. It is also
266 possible that self-sustaining populations went extinct and re-established themselves at different times in recent
267 history, since trout were introduced into rivers regardless of whether or not they were already present.
268 Nevertheless, there is no evidence for a large expansion of trout from introduction sites, and the risk of expansion
269 from current self-sustaining populations seems low.
270
271 The observation of only 10 sites with self-sustaining populations, along with the absence of expansion from these
272 sites, suggest that the environmental conditions that trout encounter after introduction or while dispersing may not
273 meet their ecological requirements well. We specifically focused on water temperature as a key factor that limits
274 the presence of trout in perennial rivers of Reunion Island, since rainbow trout are sensitive to temperature (Fausch
275 2007). These tropical rivers have a wide range of water temperatures, with higher variability among sites (spatial
276 variability) than within sites (seasonal variability). As expected, the warmest sites had no trout, while the coldest
277 sites did have them. On Reunion Island, trout experience a mean monthly temperature of 17.5°C in summer, with

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a maximum of 19.6°C. However, this study highlights a strong response to mean monthly temperature in summer (stronger than that in winter), with the estimated probability of the presence of trout decreasing from 0.95 to 0.05 as temperature increases from 16.4°C to 20.5°C, respectively.

This range differs from the optimal temperature range for rainbow trout defined in the literature (i.e. 10-16°C (Raleigh 1984; Jalabert & Fostier 2010)) but lies below the extreme of 30°C recorded in some pools in southern California, United States (Sloat & Osterback 2013). Some of the coldest sites, however, had no trout despite many introduction events. Although the probability of the presence of trout generally increased as mean monthly temperature decreased, its response differed between summer and winter, both in strength (slope) and magnitude (intercept). This result supports the hypothesis that trout temperature requirements differ between the spawning season (winter) and the growing season (summer). In the trout's native range, increasing summer temperature is a main concern for its persistence under ongoing climate change. It is predicted that higher summer temperatures will decrease the area of thermally suitable riverine trout habitats and cause them to shift upstream (Ruesch *et al.* 2012; Carlson *et al.* 2017; Isaak *et al.* 2018). In contrast, winter temperature requirements are nearly always met in temperate regions (Sloat & Osterback 2013; Brewitt & Danner 2014). On Reunion Island, the highly fragmented habitat prevents trout from dispersing upstream, or even migrating seasonally to colder and more suitable habitats. We show that in the tropics, trout may establish self-sustaining populations only at sites that have cold temperatures in both summer and winter. This result agrees with those of Scott and Poynter (1991), who concluded that high winter temperatures, rather than high summer temperatures, influenced the northern limit of trout distribution in New Zealand.

High summer temperatures may be responsible for the inability of trout to establish themselves at sites where they were introduced, since these temperatures approach the physiological limits of trout. In winter, trout require temperatures no higher than 13°C for several months for successful reproduction (Morrison & Smith 1986; Pankhurst *et al.* 1996; Jalabert & Fostier 2010), which makes winter a critical period of the life cycle. However, prolonged cold temperatures rarely occur on Reunion Island (8 out of 843 mean monthly temperatures <13°C). The relative rate of increase in summer and winter temperatures will be critical in determining the persistence and extinction risk of trout populations. This has implications for improving understanding of responses of rainbow trout to climate change in its native range. In the future, winter temperatures could become a limiting factor for trout reproduction.

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Although detailed water temperature data are rare, the presence of trout populations at high elevations in the tropics, where water temperatures are usually cooler, was no surprise. Using elevation as a coarse descriptor of trout thermal habitat, we extrapolated the results obtained from a few sites to map the probability of trout presence in a larger region. Interestingly, the thresholds of summer and winter temperatures for a given probability of the presence of trout (e.g. 0.05, 0.50, and 0.95) occurred at different elevations. Based on our simple temperature-elevation model, trout seem able to establish self-sustaining populations (0.95 probability of presence) in perennial water at 1,400 m and higher on Reunion Island. However, this is based only on the minimum temperature requirements for trout, and other key requirements that limit the presence of trout need to be considered, such as natural conditions (e.g. extreme flow regime, spawning habitat, food resources, thermal refugee) and human forcing (e.g. pollution, poaching). Furthermore, although the model described a mean variance of 77% in the data, highly contrasting geologic and topographic features can generate large differences between watersheds. For instance, the Cilaos region of Reunion Island has warmer water due to the presence of geothermal groundwater (sites 23, 36 and 37); thus, it may not be suitable for trout, despite its higher elevation. In contrast, upwelling of cool groundwater in the United States can form thermal refuges that may become critical habitat that allows trout to persist at higher temperatures (Ebersole *et al.* 2001; Sloat & Osterback 2013; Brewitt & Danner 2014). The mapping in the present study provides a broad overview of the potential presence of self-sustaining trout populations after introduction at a large scale, which we hope will be of interest to managers and policy makers. This approach of upscaling knowledge to large data-poor areas is a major challenge in ecology. It could be extended to other tropical areas to improve understanding of rainbow trout distribution and ecological regulation under warm environmental conditions. We recommend two main directions for future research: i) refine or adapt the temperature-elevation model and ii) investigate the interaction between temperature and other limiting factors to determine the ability of trout to develop self-sustaining populations in tropical rivers.

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439 TABLES

440 Table 1. Probability of rainbow trout establishing a self-sustaining population after introduction on Reunion Island

441 as a function of the introduction history.

442

Model	np	AIC	△AIC	Pseudo R^2
P(trout) ~ 1	1	38.55	0.00	0.000
P(trout) ~ Number of introduction events	2	39.89	1.34	0.018
P(trout) ~ Total number of trout introduced	2	40.01	1.46	0.014
P(trout) ~ Years since last introduction	2	40.46	1.91	0.003
P(trout) ~ Origin of trout	3	42.43	3.88	0.003

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443 Table 2. Probability of the presence of a self-sustaining population of rainbow trout on Reunion Island as a function

444 of mean monthly water temperature and season.

Model	np	AIC	△AIC	Pseudo-R^2
P(trout) ~ 1	1	621.06	137.26	0.000
P(trout) ~ Temp	2	574.03	90.23	0.076
P(trout) ~ Temp + Season	3	495.03	11.23	0.203
P(trout) ~ Temp × Season	4	483.80	0.00	0.221

445

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447 Table 3. Modeling mean monthly water temperature on Reunion Island as a function of elevation and season.

448

Model	np	AIC	△AIC	Pseudo-R^2
Temp ~ 1	1	5775.1	4426	0.000
Temp ~ Elevation	2	2886.5	1537.4	0.500
Temp ~ Elevation + Season	3	1349.1	0.00	0.766
Temp ~ Elevation × Season	4	1349.7	0.6	0.766

449

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450 FIGURE CAPTIONS

451 Fig. 1. Current distribution of rainbow trout worldwide. a) Native-distribution (green), temperate (orange) and
452 tropical (red) countries in which the species has been introduced (adapted from Crawford and Muir (2008). b)
453 Results of introducing rainbow trout into tropical countries: evidence of the presence of self-sustaining populations
454 in 1988 (in the review by Welcomme (1988), light blue) and after 1988 (dark blue), no information available about
455 the presence of self-sustaining populations (light green), and no evidence of self-sustaining populations (dark
456 green). See Table S1 for supporting information and references.

457

458 Fig. 2. Map of Reunion Island showing perennial rivers and the location and introduction effort at 33 sites where
459 rainbow trout were introduced from 1940-2019. The number of introduction events, used as a proxy of the effort,
460 is represented by increasing shades of gray. The star symbol represents an introduction site with unknown effort.
461 See Table S2 for more information about the sites.

462

463 Fig. 3. Mean monthly water temperatures at 35 sites on perennial rivers on Reunion Island. Colors show the sites
464 where attempts to introduce rainbow trout resulted in self-sustaining populations (green) or were not successful
465 (red), and sites with no introduction events (gray). See Table S2 for details of the temperature data.

466

467 Fig. 4. Mean probability of the presence of rainbow trout on Reunion Island (± 1 standard error) as a function of
468 mean monthly water temperature and season (winter (blue) or summer (yellow)). The solid lines are estimates of
469 the Mtemp model (Table 2), and circles are raw data. The dashed lines represent 0.95, 0.50 and 0.05 probabilities
470 of the presence of trout, from top to bottom.

471

472 Fig. 5. Winter and summer water temperatures at 35 sites on Reunion Island. Colors show the sites where attempts
473 to introduce rainbow trout resulted in self-sustaining populations (green) or were not successful (red), and sites
474 with no introduction events (gray). The dashed lines represent estimated thresholds of water temperatures for 0.95,
475 0.50 and 0.05 probabilities of the presence of trout, from top to bottom. Sites are ordered by increasing elevation.
476 Whiskers represent 1.5 times the interquartile range. See Table S2 for more information about the sites.

477

478 Fig. 6. Relationship between mean monthly water temperature and elevation in winter (blue) and summer (yellow)
479 on Reunion Island. The solid lines are model estimates (Table 3), and the gray circles are raw data.

480

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481 Fig. 7. Map illustrating the predicted probability of the presence of self-sustaining populations of rainbow trout
482 after introduction into all perennial rivers on Reunion Island. Circles show the location of 33 sites where rainbow
483 trout were introduced and are absent (circled black point) or present (circled black cross).

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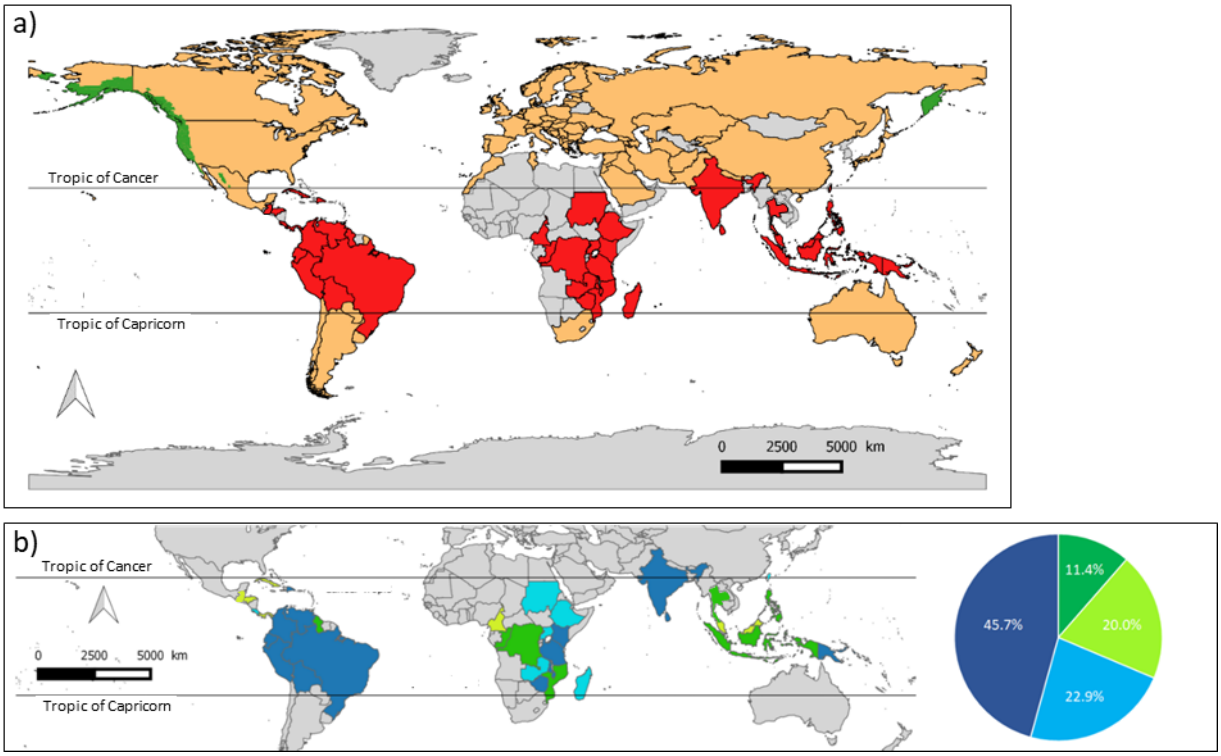
a)

484 FIGURES



485

486 Figure 1

487

b)

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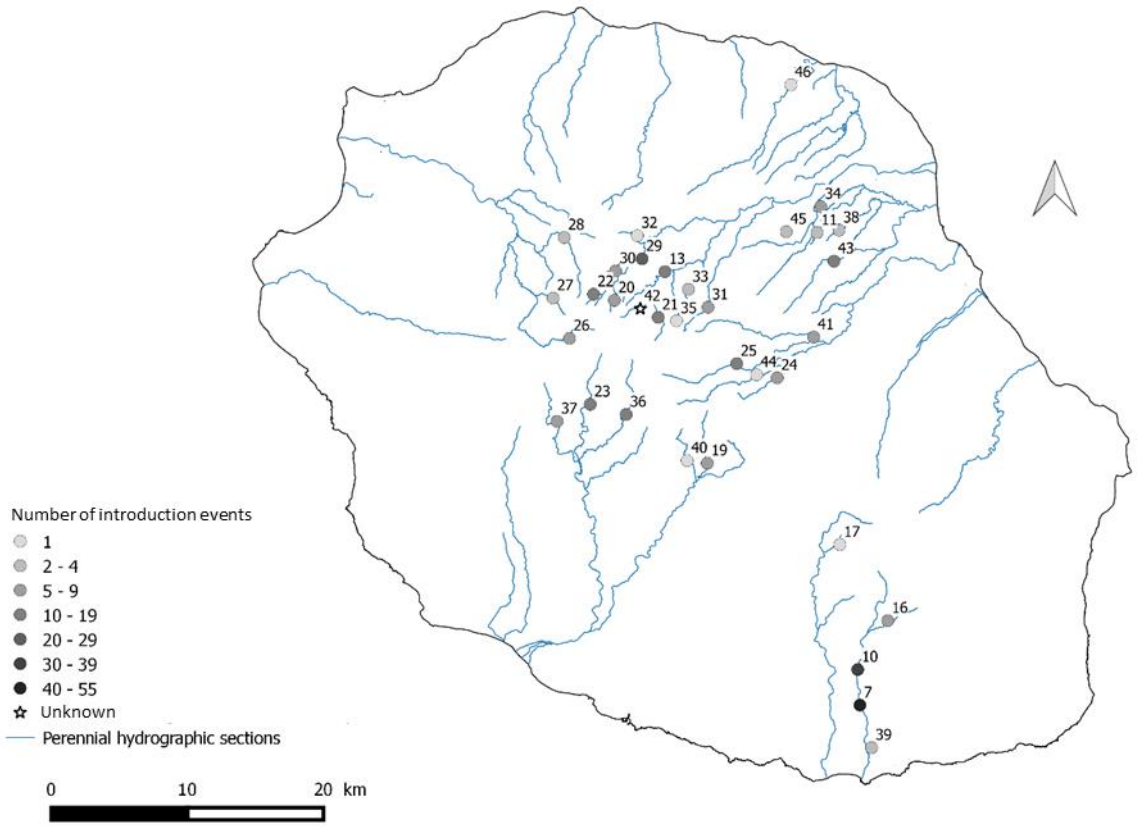

Figure 2

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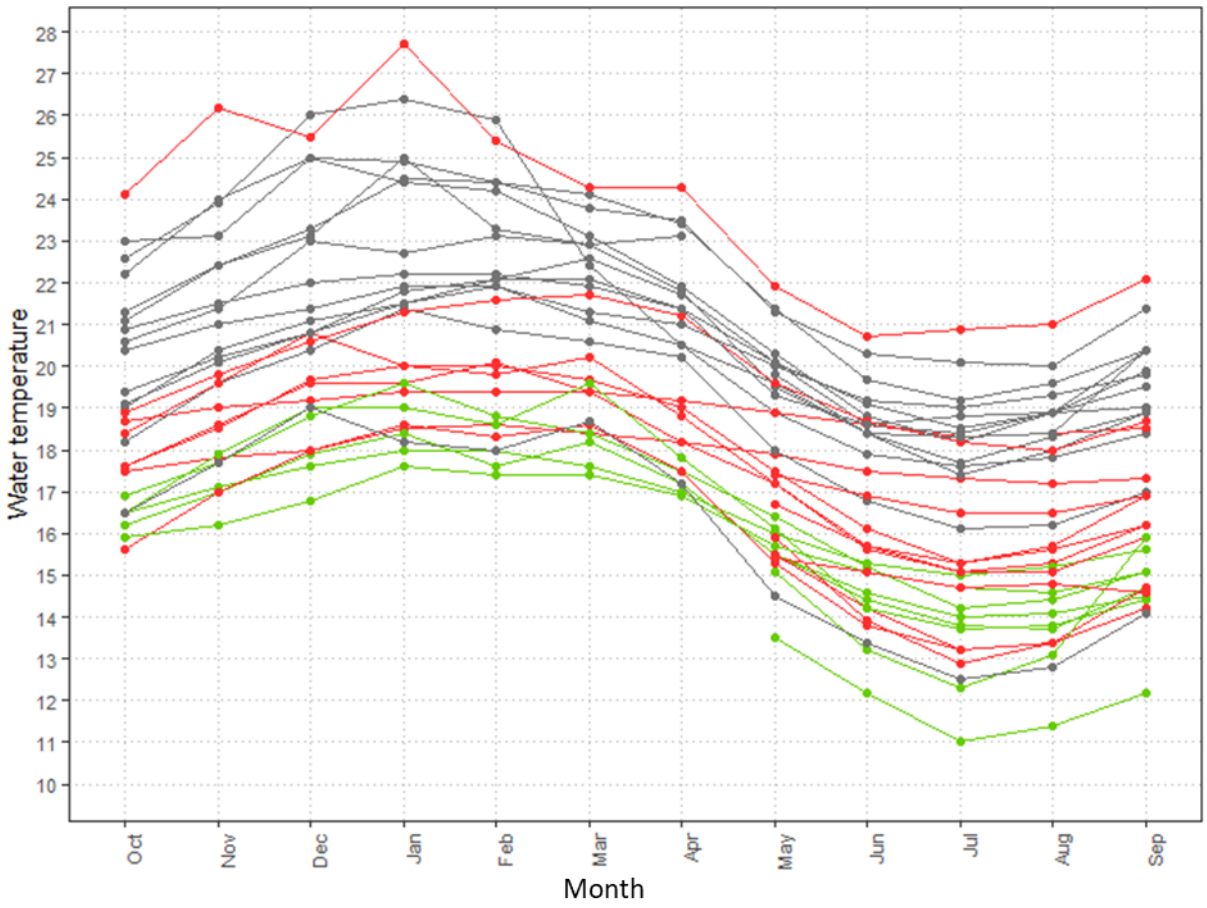

492

493 Figure 3

494

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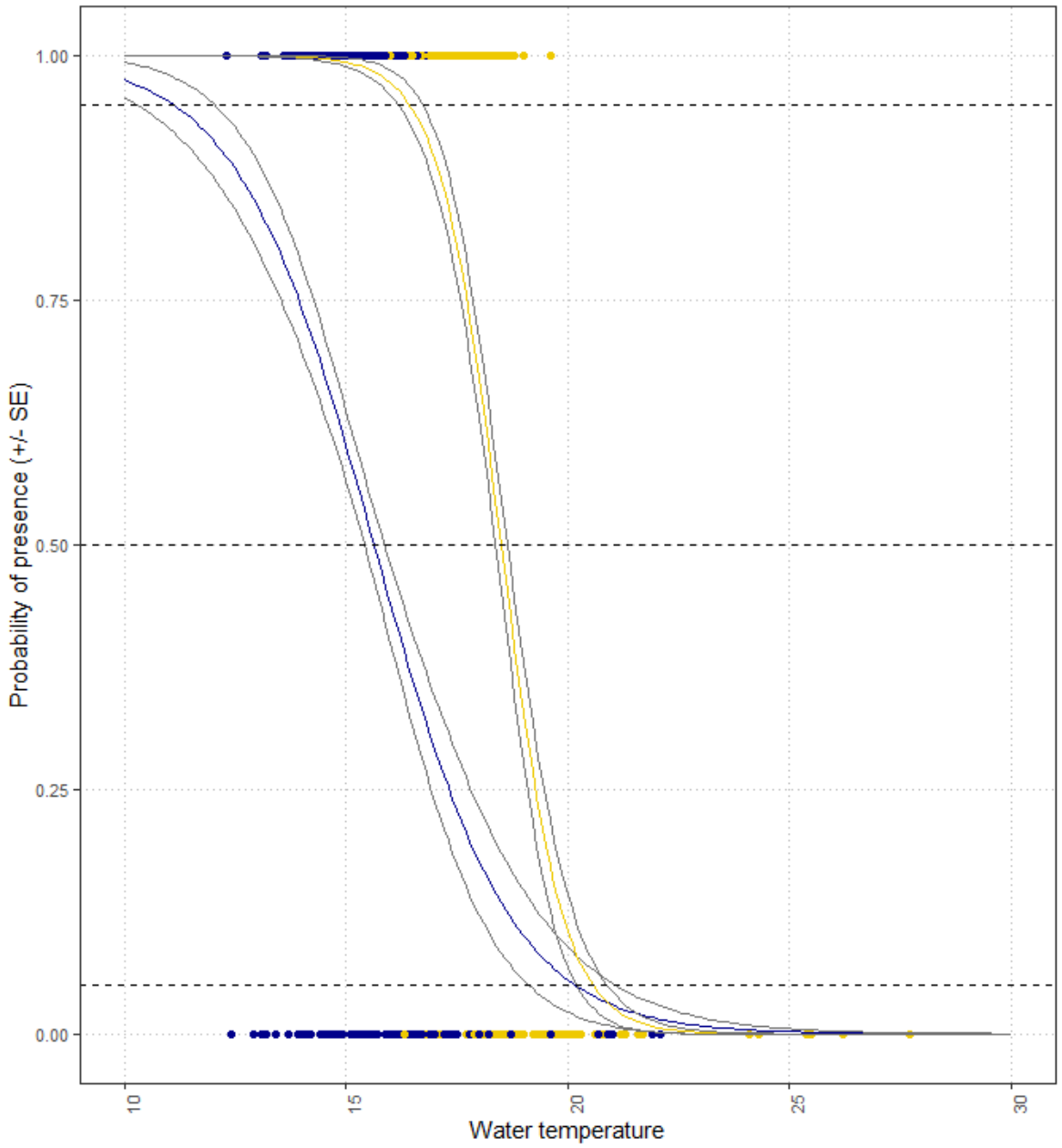

Figure 4

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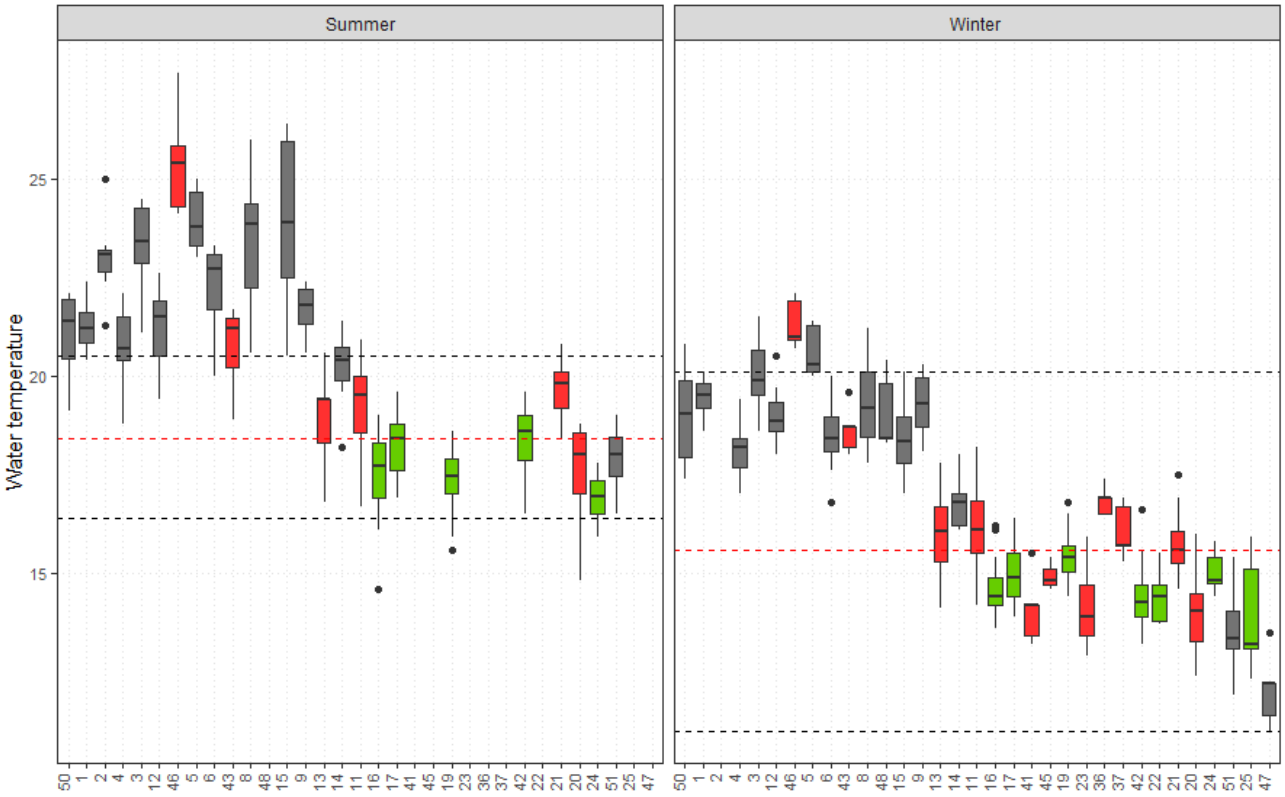

Figure 5.

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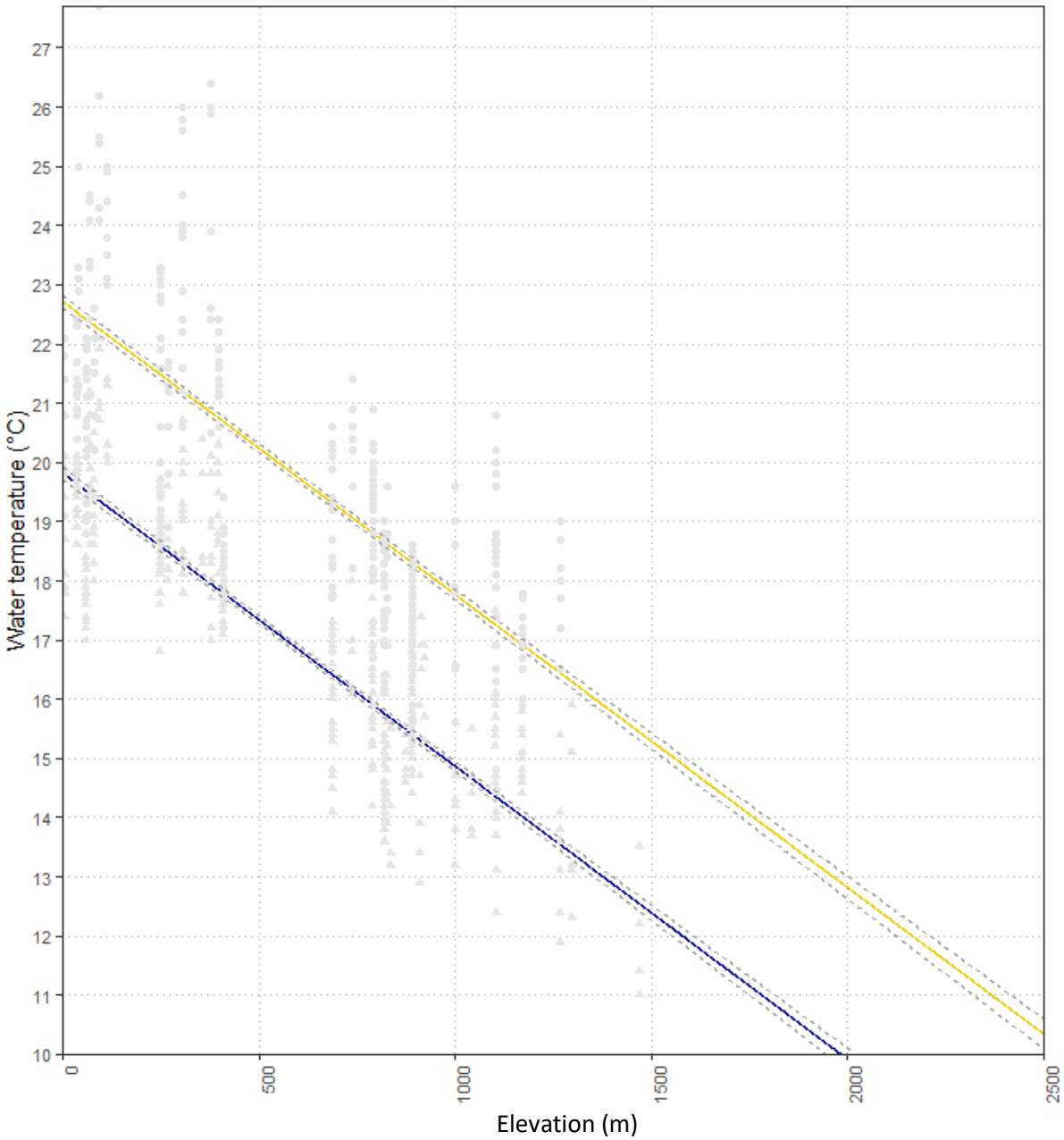

Figure 6

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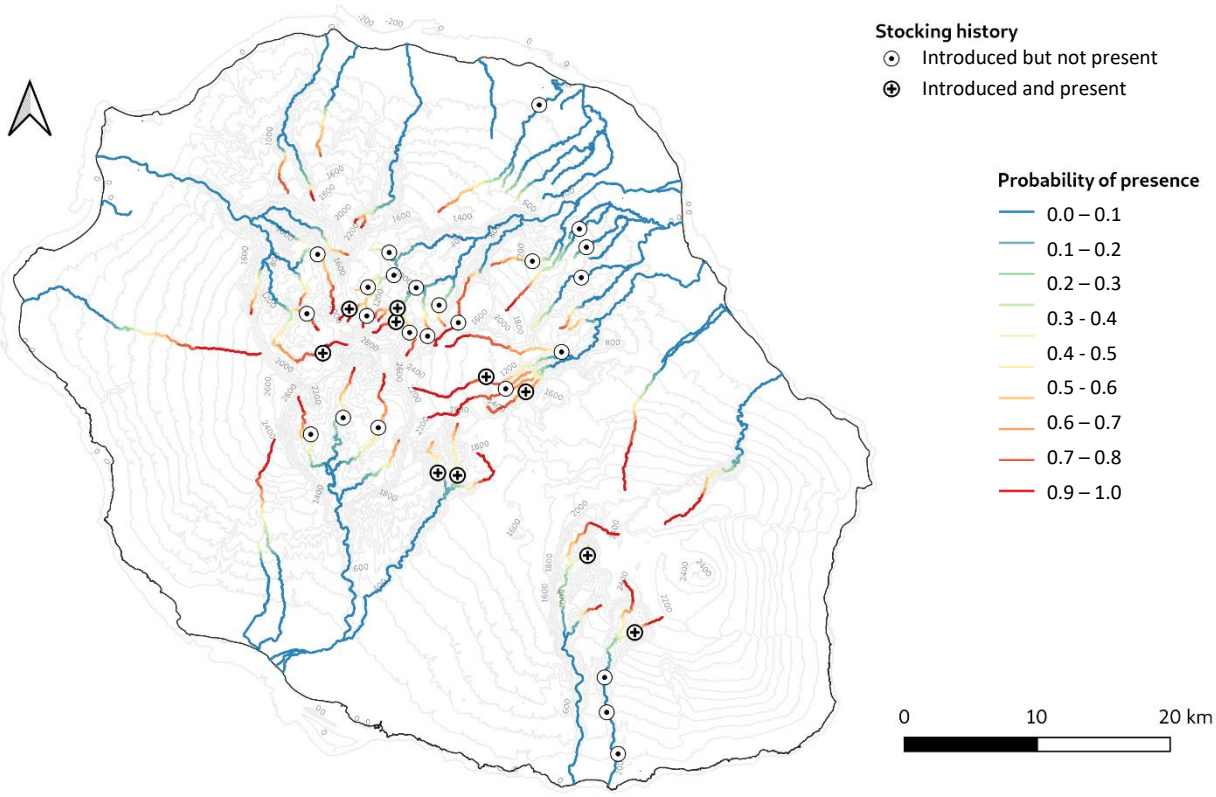

504

505 Figure 7

506