The legacy of over a century of introductions: Spread debt of rainbow trout (*Oncorhynchus mykiss*) in Mpumalanga Province, South Africa

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ABSTRACT

For over a century, rainbow trout (*Oncorhynchus mykiss*) has been widely introduced into lakes and rivers in South Africa to create and enhance sport-fishing opportunities. Despite its long history of introduction, naturalized populations of rainbow trout are still localized to a few areas with suitable habitats and climate. This study assessed the spread debt (i.e., the increase in area invaded by invasive species over time) of rainbow trout in Mpumalanga Province, South Africa to highlight areas with known introductions, the extent of the invasion, and to identify areas that are suitable for establishment but are still invasion-free. The total river length that was predicted as suitable for rainbow trout under current climate was about *ca*. 3,500 km in an extension of about *ca*. 15,000 km. Current occupancy (river length predicted as suitable with known rainbow trout occurrence records) was *ca*. 1,220 km (35%) and the invasion debt was therefore estimated as 65%. While these data infer a large invasion debt, they are confounded by a lack of knowledge on sampling effort and verified true absence and should therefore be recognized as an estimate. In addition, the extent of the suitable area varied under different climate change scenarios where it was projected to decrease under RCP 4.5 scenarios and increase under the RCP 8.5 scenarios. This study demonstrates some of the difficulties of quantifying the potential future extent and impacts of biological invasions and how the invasion debt concept can be applied to provide an important link between invasion biology, management, and policy.

KEYWORDS: biological invasions, climate change, conservation, species distribution modeling, spread

1 INTRODUCTION

Biological invasions are a threat to biodiversity, ecosystems, and the services they provide, human livelihoods and health (IPBES, 2019). One of the major challenges in managing biological invasions is the difficulty in quantifying their potential future extent and impacts

(McGeoch et al., 2010; Pereira et al., 2013; Richardson & Pyšek, 2012). This is especially a concern when the number of new introductions has rapidly increased over the last two centuries due to increasing global connectivity (Seebens et al., 2018). The high proportion of recently introduced alien species whose future impacts are difficult to predict is likely to lead to an increase in challenges associated with biological invasions, an important aspect of a phenomenon known as "invasion debt" (Essl et al., 2011; Rouget et al., 2016). Invasion debt consists of (a) introduction debt (i.e., the number of new alien species that will be introduced to a region if no action is taken); (b) establishment debt (i.e., the number of alien species that will become invasive in future); (c) spread debt (i.e., the increase in area invaded by invasive species over time); and (d) impact debt (i.e., the increase in impacts due to the invasion over time; Rouget et al., 2016).

The invasion debt concept is widely applied to provide an important link between biological invasions, management, and policy. For example, establishment debt can be used to identify new invasions that have implications for the development of post-border biosecurity and implementation measures to prevent the spread of potential invasive species (see Seebens et al., 2018). Spread debt can be used to identify additional areas that are likely to be invaded, and management implications include the identification of priority areas for control, the identification of areas where spread reduction methods are required, and spatial planning of the management of biological invasions (e.g., Khosa, Marr, Wasserman, Zengeya, & Weyl, 2019; Padayachee, Procheş, & Wilson, 2019). There are few studies that have investigated some aspects of invasion debt in South Africa, such as establishment debt (e.g., Faulkner, Robertson, Rouget, & Wilson, 2016; Novoa, Kaplan, Kumschick, Wilson, & Richardson, 2015; Walker, Gaertner, Robertson, & Richardson, 2017), spread of single species (e.g., Moore, Runge, Webber, & Wilson, 2011), and only one study has investigated all four components of invasion debt (Rouget et al., 2016).

Trout is a common name for several freshwater fish species from three genera within the family Salmonidae (Cuvier, 1816) comprising *Oncorhynchus* Suckley, 1861, *Salmo* Linnaeus, 1758, and *Salvelinus* Richardson, 1836. Several trout species have been globally introduced to areas outside their natural ranges to enhance angling opportunities and for aquaculture (Cambray, 2003; Crawford & Muir, 2008; Stanković, Crivelli, & Snoj, 2015). In South Africa, there are four salmonid species that have been introduced and these include *Oncorhynchus mykiss* (Walbaum, 1792) (rainbow trout), *Salmo salar* Linnaeus, 1758 (Atlantic salmon), *Salmo trutta* Linnaeus, 1758 (brown trout), and *Salvelinus fontinalis* (Mitchill, 1815) (brook trout) (Ellender, Woodford, Weyl, & Cowx, 2014; Marr et al., 2017). The introductions of Atlantic salmon and brook trout were not successful, probably due to lack of suitable habitats, but brown and rainbow trout have naturalized in several mountain headwater streams in the country (Ellender et al., 2014). This can be attributed to sustained and widespread stocking for sport fishing, initially by government agencies and later by angling societies and private individuals, and a pre-selection of suitable receiving environments that are similar to the species' native ranges (de Moor & Bruton, 1998; Ellender et al., 2014).

For cold water species such as trout, climate change events such as global warming are likely to decrease habitat availability through range constriction of suitable areas (Comte, Buisson, Daufresne, & Grenouillet, 2013; Isaak et al., 2010). The invasibility of a given area is partly influenced by climatic suitability of the recipient habitat to the invader (Lim, Choi, Jeon, Son, & Lee, 2018; Shelton et al., 2018). Climate change can therefore be a critical factor in determining the potential range of rainbow trout. Climate change has been implicated in changes to precipitation patterns, intensity, and an increase in the frequency and magnitude of extreme events such as droughts and flooding (Bates, Kundzewicz, Wu, & Palutikof, 2008). Changes in precipitation and water temperature influence the availability of surface water, habitats, and food resources (Lowe-McConnell, 2000), which in turn, affect the abundance, composition, distribution, productivity, and phenology of aquatic species (e.g., Argent & Kimmel, 2013; Bates et al., 2008; Comte et al., 2013; Junker et al., 2015).

The main objectives of this study were to predict the extent of rainbow trout invasions in the river systems in Mpumalanga Province, South Africa, and project how current and future climatic scenarios are likely to affect its potential invasive range. Rainbow trout was introduced into local streams and rivers in the province as early as 1910 and it is currently known to occur in several upland areas of the province where it supports aquaculture and sport fishing (McCafferty, Ellender, Weyl, & Britz, 2012). Despite its long history of introduction, naturalized populations of trout are still localized to a few areas with suitable habitats and climate. In other areas, water temperatures are only suitable during certain periods of the year and populations need to be maintained through stocking (Rivers-Moore, Ellender, & Weyl, 2019). We hypothesized that rainbow trout has a low invasion debt because sustained and widespread stocking in pre-selected suitable receiving environments has allowed it to establish in most of the areas that it has been introduced, but climate change is likely to lead to a range constriction because of increasing temperatures.

2 METHODS

2.1 Species distribution modeling

Current and future suitable areas for rainbow trout were predicted using species distribution modeling (SDM) with Maxent based on climatic variables (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). Maxent uses the association between environmental variables and species occurrence data to predict areas that are climatically suitable (Phillips, Andersonb, & Schapired, 2006). The approach has been widely applied to predict species distribution of freshwater fish (e.g., Khosa et al., 2019; Lübcker, Zengeya, Dabrowski, & Robertson, 2014; Zengeya, Booth, & Chimimba, 2015; Zengeya, Robertson, Booth, & Chimimba, 2013), and in a range of biological disciplines such as ecology and evolutionary biology (e.g., Elith & Leathwick, 2009; Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Kearney & Porter, 2009), impacts of climate change (e.g., Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009), and biological invasions in general (e.g., Broennimann & Guisan, 2008; Townsend & Vieglais, 2001).

2.2 Current bioclimatic data

The environmental variables used to train the SDM consisted of 19 widely used bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; https://www.worldclim.org/data/v1.4/worldclim14.html) downloaded at a spatial resolution of 30 arc sec. The bioclimatic variables represent annual forecast (e.g., annual mean temperature and annual precipitation, seasonality, mean temperature of the warmest month, mean temperature of the warmest quarter, and precipitation of the wettest quarter), and extreme environmental variables (e.g., temperature of the coldest and warmest month and precipitation of the wet and dry quarters). The selection of variables used to train the model can influence model performance and various methods have been used to pre-select variables (Elith et al., 2011; Zengeya et al., 2015). The current study used an iterative process to evaluate the influence of bioclimatic variable selection on model performance (Zengeya et al., 2015). The first approach took advantage of the in-built regularization in Maxent that deals with the selection of bioclimatic variables (regulating some to zero). This process has been shown to perform well and is considered to outperform other pre-selection procedures (Elith et al., 2011). A Spearman correlation analysis was then used to check for correlated variables (>0.8; Dormann et al., 2012). Variable contribution to model performance was then checked by jack-knife analysis for each pair of correlated variables. The second approach only used variables that were pre-selected using correlation and jack-knife analysis. However, the in-built regularization method outperformed the preselection procedure, and it was therefore used for proximal variable selection.

2.3 Species data

Occurrence data for rainbow trout were obtained from the GBIF: Global Biodiversity Information Facility (https://www.gbif.org/occurrence/download?q=Oncorhynchus%20mykiss, accessed July 13, 2021), South African Institute of Aquatic Biodiversity (SAIAB), and Mpumalanga Tourism and Parks Agency (MTPA). The occurrence records were obtained from both native and introduced ranges of rainbow trout in order to achieve a better estimation of the species realized niche. The occurrence records were also checked for duplicate records and inaccurate coordinates (e.g., some records were not properly geo referenced and where on sea instead of inland freshwater systems). In addition, records that had no geographical coordinates were also removed. This decreased the number of occurrence points in the final data set from 120,707 to 15,917 records (Table S1). The occurrence records were, however, biased toward the native range. To prevent over representation of the associated environmental conditions in the native range, a preliminary analysis was undertaken to check for autocorrelation. This was achieved by spatially rarefying the occurrence data at 1°, 2°, 3°, 4°, and 5° using the SDM-toolbox in ArcGIS (Brown, 2014). The best model performance was obtained with data spatial rarefied to 1° (972 records), and this spatial resolution was then used to run the final models.

2.4 Model building

Several modeling standards have been proposed that recommend the use of multiple techniques when modeling species distributions (e.g., Araújo et al., 2019). However, single statistical methods such as Maxent might be more appropriate when simple models are used. A Maxent model with only hinge features selected has been shown to outperform other more complex models when modeling the distributions of alien species (Elith, Kearney, & Phillips, 2010). In addition, the performance of consensus models built from multiple approaches varies and it is still unclear on whether these consensus models perform better than the individual models they comprise (Hao, Elith, Guillera-Arroita, & Lahoz-Monfort, 2019). Therefore, in this study, a single statistical approach (Maxent) was used to model species distribution. Models were optimized using the following parameters: (a) a maximum number of 500 iterations; (b) a regularization multiplier of 1; (c) convergence threshold of 0.00001; (d) only hinge features selected. Clamping was selected to ensure that the models are not predicting into areas that had dissimilar environments to the selected background localities (Merow, Smith, & Silander, 2013).

Maxent uses presence-only data and background localities to project potential suitable areas (Merow et al., 2013). The extent of this background is known to influence model performance, where a broad background can cause overestimates and a constrained background can cause underestimates (Van Der Wal, Shoo, Graham, & Williams, 2009). In the current study, the background was limited to areas with similar climate to known occurrence records of rainbow trout in both its native and introduced ranges. This was undertaken by overlaying the Köppen–Geiger climate classification system with the known distribution, following Thompson et al. (2011). Köppen–Geiger polygons indicate areas with similar climates and a given climate zone was included as part of the background if it contained an occurrence record within the range of rainbow trout using ArcMap® 10.4 (ArcGIS™; ESRI®, Redlands, CA). By selecting the entire climatic zone, an intermediate background size was obtained, compensating for areas in the introduced ranges that had few occurrence records (Van Der Wal et al., 2009). Each model was then calibrated with 10,000 pseudo-absence points randomly obtained from the defined background (Phillips & Dudík, 2008). Model evaluation was done using cross validation, where occurrence records were randomly partitioned into a calibration set (training set) and a testing set (validation set) using k-fold partitioning (Phillips et al., 2006). Average model performance was obtained by repeating the process for 10 iterations after which a consensus map was then created. Several different methods have been used to select thresholds of occurrence, and the choice of an appropriate method is dependent on type of data that is available and questions the study intends to address (Liu, Newell, & White, 2016; Pearson, 2007). In this study model output was set to logistic format and an equal training sensitivity and specificity threshold rule was applied where areas with a probability ≥0.5 were taken as climatically suitable and those below were taken as not suitable. Rainbow trout is a cold-water species that has a restricted range in South Africa where it occurs only in areas that experience low water temperatures (10–20°C; Rivers-Moore et al., 2019; Weyl et al., 2020). A high threshold value (0.5) was therefore chosen to minimize the risk of identifying unsuitable sites by identifying only areas with highest suitability (Pearce & Ferrier, 2000; Pearson, 2007).

2.5 Model evaluation

The performance of the model was assessed using a receiver operating characteristic curve (ROC) which measures the discrimination ability (between presence and background) of the models where values ≤0.5 indicate random predictions and values between 0.8 and 1.0 indicate acceptable predictions (Swets, 1988). Model performance was assessed as fair (when AUC values were between 0.8 and 0.9), good (0.9–0.95), and excellent (>0.95), following Thuiller, Lavorel, Sykes, and Araújo (2006). Although the AUC statistic has been widely used to validate niche models (Elith et al., 2011; Phillips et al., 2006), it is not necessarily an appropriate measure for presence-only model evaluation (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). Consequently, model performance was further assessed using the Continuous Boyce Index (CBI) (Boyce et al., 2002). The CBI evaluates the ability of habitat suitability models to predict the presence of a species in a given area. It is continuous, and values may range from −1 to 1, with negative values indicating models that predict worse than random, and the positive values indicating models that are consistent with presence distribution in the evaluation data set.

2.6 Climate change

Climate change models were built using projected climate data for 30 years (2050: 2041–2060) and 50 years (2070: 2061–2080) that were obtained from recent climate projections by the IPCC Fifth assessment Report (IPCC, 2014). The data used were downloaded under one Global Climate Models (Access-1.0, CSIRO-BOM, Australia; http://www.worldclim.org). For each period, the data were simulated under two Representative Concentration Pathways (RCPs) scenario, RCP 4.5 and RCP 8.5. The scenarios were selected to make a comparison between a scenario that is likely to occur (RCP 4.5) and a worst-case scenario that is highly unlikely to occur (RCP 8.5; Hausfather & Peters, 2020). The RCP 4.5 scenario represents CO_2 emissions that stabilize without overshoot to ~650 ppm by 2100, whereas RCP 8.5 represents CO_2 emissions that continued to rise under current trajectory to ~1,370 ppm by 2100 (Moss, Edmonds, & Hibbard, 2010). Under the RCP 4.5 scenario, temperature is predicted to increase by between 0.9–2°C in 2050 and 1.1–2.6°C in 2070, while under the RCP 8.5 scenario, it is projected to increase by 1.4–2.6°C in 2050 and 2.6–4.8°C in 2070 (IPCC, 2014). These scenarios have previously been used to predict the potential impact of climate change on fish distribution (e.g., Merriam, Fernandez, Petty, & Zegre, 2017; Shechonge, Ngatunga, & Bradbeer, 2019). Bioclim variables for the two climate models and emission scenarios were obtained from Worldclim v.1.4 (Hijmans et al., 2005; https://www.worldclim.org/data/v1.4/worldclim14.html). Variables were downloaded at a spatial resolution of 30 arc sec and were prepared in ArcMap® 10.4 (ArcGIS™; ESRI®, Redlands, CA). Models were then developed using the same methods as outlined for current climate models.

2.7 Area-based invasion debt under current climate

Area-based invasion debt represents the difference between the area where a species is currently known to have established (i.e., occupancy) and areas that are predicted to be climatically suitable but are still invasion-free (Rouget et al., 2016). For species that are already invasive in a region, area-based invasion debt is composed of (a) the climatic suitability of a region for each species and occupancy; and (b) the rate of spread (both natural and human-mediated) of that species (Rouget et al., 2016).

A deductive qualitative threshold was used to assess the current introduction status of rainbow trout in South Africa following Khosa et al. (2019). Rainbow trout were considered invasive in the country because there are known to have naturalized in more than 10% of the quaternary catchments. Niche models were then used to delineate areas that were climatically suitable for rainbow trout under current climate.

Occupancy was inferred from areas designated as trout areas by the Mpumalanga Nature Conservation Act No. 10 of 1998 and the Department of Forestry, Fisheries and the Environment-South African National Biodiversity Institute (DFFE-SANBI) consultative mapping areas exercise that delineated areas where rainbow trout was known to occur in Mpumalanga Province. The Department of Forestry, Fisheries, and the Environment (DFFE) initiated a mapping exercise in consultation with provincial conservation authorities, angling agencies, and the aquaculture industry to delineate areas where trout are known to occur. The main tenant for this mapping process was that utilization of rainbow trout will be allowed in areas where it has naturalized and in areas where it has been historically stocked for a put and take fishery. These maps should, however, be viewed with a low degree of confidence because they are based on expert opinion and have not been verified through a formal mapping process that is based on recent surveys with adequate ground-truthing.

The river length (km) that is suitable for rainbow trout under current climate conditions and with known rainbow trout occupancy (river length in quaternary catchments with known occurrence records from the mapping exercise) was then derived and extracted from the SDMs in each quaternary catchment and designated a value of 1, and a 0 was designated to river streams without known occurrence for rainbow trout. River segments that were predicted as unsuitable but had known rainbow trout occupancy were not considered in the area-based invasion debt calculations. The South African River shapefile (scale 1:500,000) was

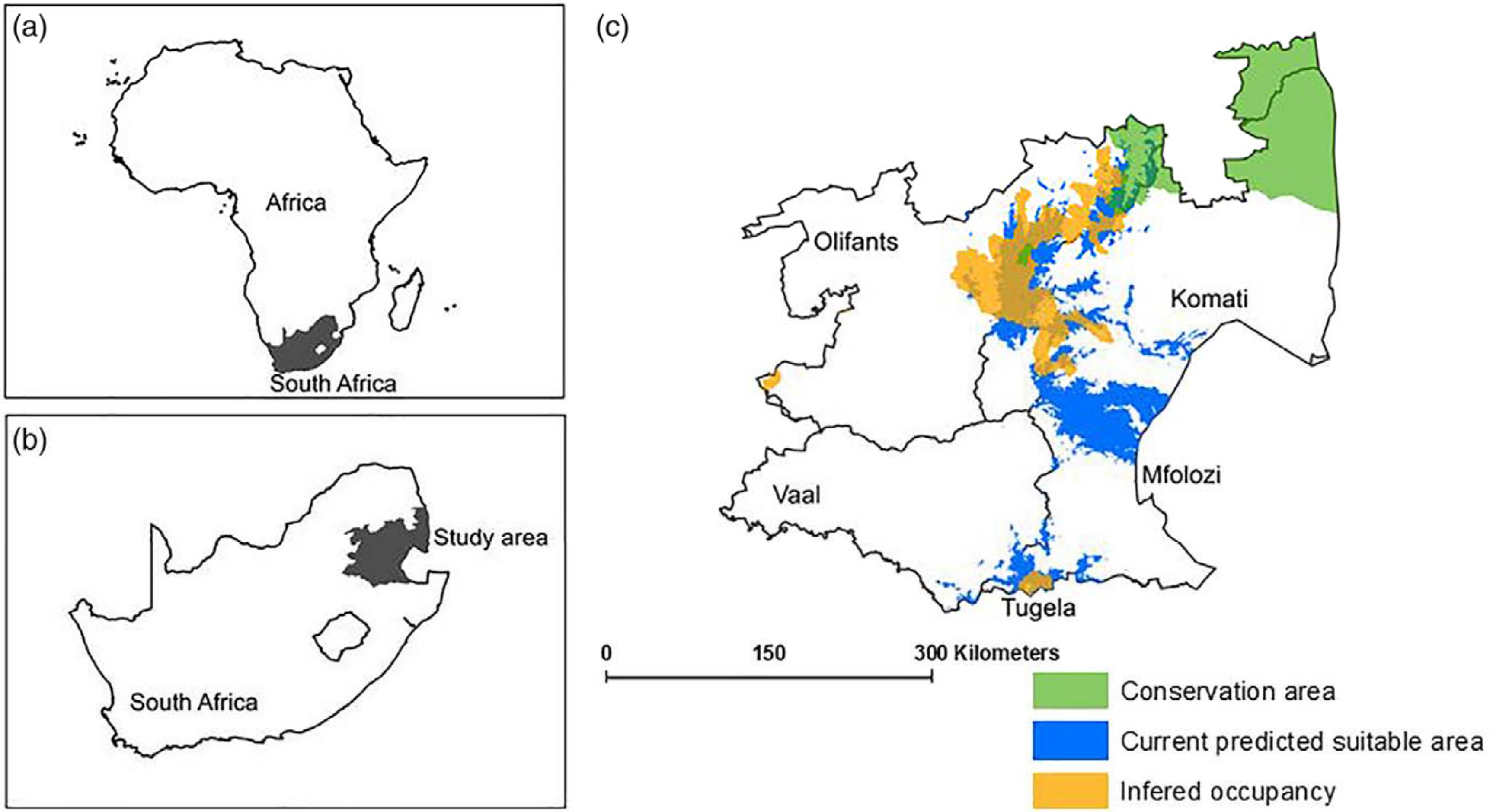

FIGURE 1. The predicted distributional range of rainbow trout (*Oncorhynchus mykiss*) across five Water Management Areas (Komati, Mfolozi, Olifants, Vaal, and Tugela) in Mpumalanga Province, South Africa. Areas with predicted suitable conditions are indicated by blue, current distribution (occupancy) of rainbow trout in yellow, and protected conservation areas in green

TABLE 1. Bioclimatic variables and their percentage contribution to model performance for predicted distributional range of rainbow trout (*Oncorhynchus mykiss*) under current and future (2050 and 2070) climatic conditions in Mpumalanga Province, South Africa

Climatic variables	Current climate	2050		2070	
		RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
BIO1 = annual mean temperature	9.6	4.7	1.2	2.0	3.0
BIO2 = mean diurnal range (mean of monthly [max temp – min temp])	0.8	1.1	1.4	1.1	1.7
BIO3 = Isothermality (BIO2/BIO7) (* 100)	36.6	37.3	69.0	53.6	53.3
BIO4 = temperature seasonality (standard deviation * 100)	0.9	0.3	0.9	1.5	1.4
BIO5 = max temperature of warmest month	0.9	0.6	1.4	0.6	1.1
BIO6 = min temperature of coldest month	0.8	17.0	0.5	3.7	0.5
BIO7 = temperature annual range (BIO5-BIO6)	1.0	0.6	1.7	0.7	0.7
BIO8 = mean temperature of wettest quarter	0.8	2.0	0.2	2.0	0.3
BIO9 = mean temperature of driest quarter	0.4	0.1	0.9	0.2	0.3
BIO10 = mean temperature of warmest quarter	2.9	1.7	0.6	1.4	1.3
BIO11 = mean temperature of coldest quarter	36.7	27.8	6.7	27.1	30.3
BIO12 = annual precipitation	0.0	0.0	0.3	0.0	0.1
BIO13 = precipitation of wettest month	0.3	0.4	0.3	0.3	0.1
BIO14 = precipitation of driest month	0.4	0.1	0.3	0.0	0.2
BIO15 = precipitation seasonality (coefficient of variation)	0.3	0.3	0.3	0.7	0.5
BIO16 = precipitation of wettest quarter	0.4	0.2	0.6	0.1	0.1
BIO17 = precipitation of driest quarter	0.0	0.0	0.1	0.0	0.0
BIO18 = precipitation of warmest quarter	0.8	0.8	0.2	0.3	0.3
BIO19 = precipitation of coldest quarter	6.2	5.0	13.5	4.6	4.8

Note: Two Representative Concentration Pathways (RCPs) scenarios (RCP 4.5 and RCP 8.5) were used to build the future climate change models.

downloaded from the Department of Water Affairs, South Africa (http://www.dwaf.gov.za/iwqs). The area-based invasion debt analysis was undertaken using ArcMap® 10.4 (ArcGIS™; ESRI®, Redlands, CA).

3 RESULTS

3.1 Current climate

The areas that were predicted as climatically suitable for rainbow trout were mainly located in quaternary catchments in the Olifants and Komati Water Management Areas (Figure 1). Model performance was good (AUC = 0.94; CBI = 0.9) and the bioclimatic variables that contributed most to model performance were mean temperature of the coldest quarter (37%), isothermality (37%), and annual mean temperature (10%) (Table 1). The response curves indicated that the areas indicated as climatically suitable for rainbow trout had a mean temperature of the coldest quarter that ranged between −14 and 4°C, isothermality (28–46), and annual mean temperature (4–15°C) (Figure S1). The variable with the most useful information by itself was the mean temperature of coldest quarter, and the variable with the most information that was not present in the other bioclimatic variables was isothermality (Figure S2).

3.2 Current climate area-based invasion debt

The total river length that was predicted as suitable for rainbow trout was *ca*. 3,500 km in a river extension of *ca*. 15,000 km (Table 2). Current occupancy (river length that were predicted as suitable and have known rainbow trout occurrence records) was about 1,300 km (35%) and the invasion debt was therefore estimated as 65% (Figure 1). The river length predicted as unsuitable was about 11,400 km in a river extension of 15,000 km with an occupancy of about 720 km (6% of the unsuitable area).

TABLE 2. The extent of river length that is predicted as suitable for rainbow trout (*Oncorhynchus mykiss*) under current and future (2050 and 2070) climatic conditions in Mpumalanga Province, South Africa

Climate scenario	Predicted suitable river length (km)	Predicted suitable river length (km) in conservation area
Current	*ca*. 3455.8	*ca*. 431.6
RCP 4.52050	*ca*. 1142.6	*ca*. 188.1
RCP 4.52070	*ca*. 2989.6	*ca*. 489.6
RCP 8.52050	*ca*. 6285.7	*ca*. 678.6
RCP 8.52070	*ca*. 4149.7	*ca*. 532.3

Note: Two Representative Concentration Pathways (RCPs) scenarios (RCP 4.5 and RCP 8.5) were used to build the future climate change models.

3.3 Projected impact of climate change on the introduced range

The river length that was predicted as suitable for rainbow trout in the current climate (*ca*. 3,500 km) is projected to decrease by 67% in 2050 and by 14% in 2070 under the RCP 4.5 scenario (Figure 2a,b). In contrast, projections under the RCP 8.5 scenarios showed an overall increase in the extent of suitable area of 81% in 2050 and 20% in 2070 (Figure 2c,d). The extent of river length suitable for rainbow trout in conservation areas is expected to increase from 13% (*ca*. 450 km) in the current climate to over 14% in all the future RCP scenarios except for RCP 4.5 in 2050 (Table 2). Additional information on variable contribution to model performance is provided in Figures S3–S10.

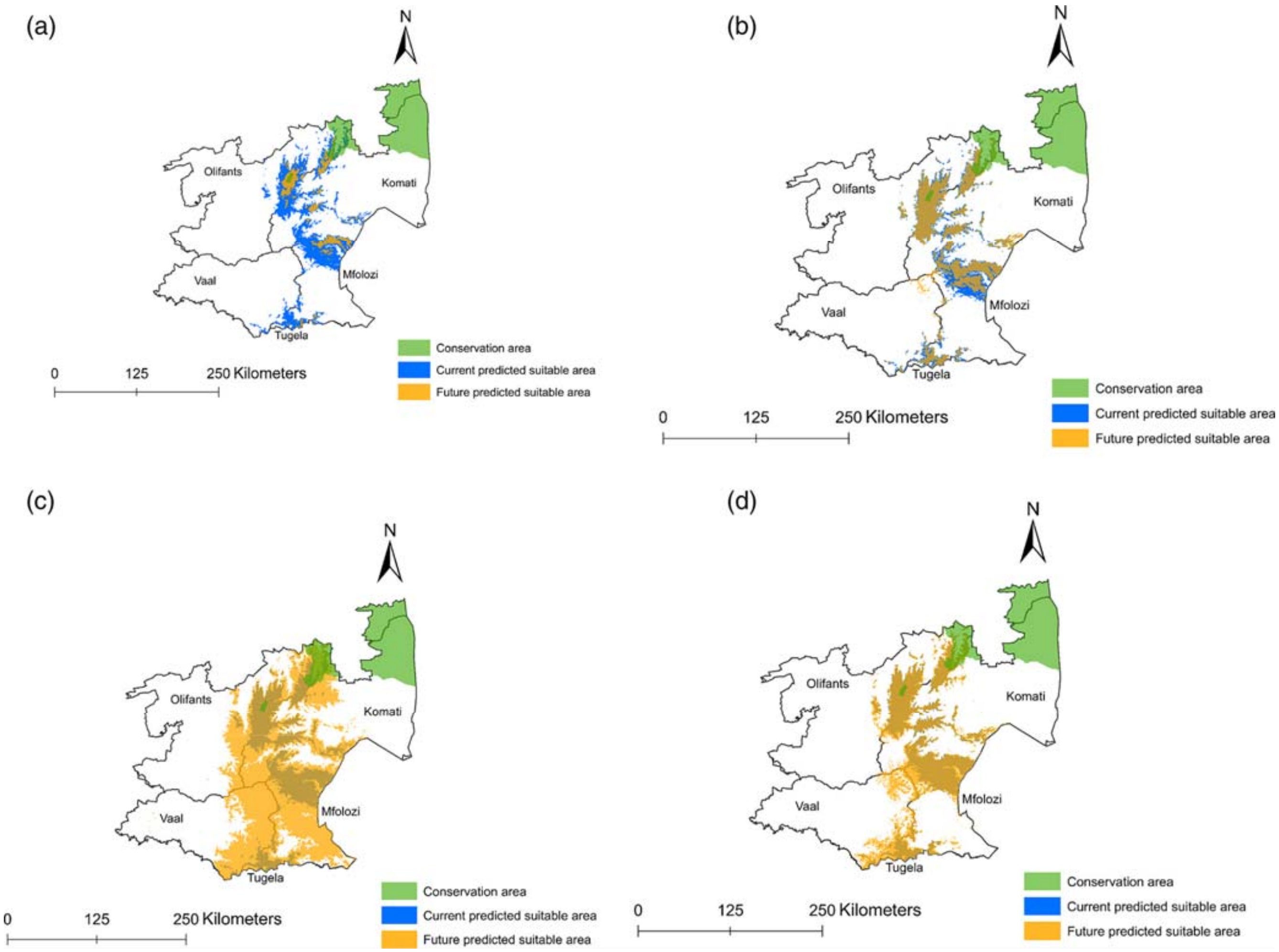

FIGURE 2. Projected changes in the extent of areas that were predicted as climatically suitable for rainbow trout (*Oncorhynchus mykiss*) in Mpumalanga Province, South Africa between 2050 and 2070 based on two Representative Concentration Pathways (RCP 4.5 and 8.5) scenarios: (a) RCP 4.5 (2050), (b) RCP 4.5 (2070), (c) RCP 8.5 (2050), and (d) RCP 8.5 (2070)

4 DISCUSSION

This study evaluated the extent of rainbow trout invasion in river systems in Mpumalanga Province, South Africa and assessed how current and future climatic scenarios could affect its potential invasive range. The study evaluated the hypothesis that rainbow trout has a low spread debt in the Mpumalanga Province because sustained and widespread stocking in pre-selected suitable receiving environments might have allowed the species to establish in most of the areas where it has been introduced. There was no evidence to support this assertion, instead rainbow trout had a high invasion debt, and it has not established in most areas that were predicted as climatically suitable under current climate.

The predicted potential geographical range of rainbow trout in Mpumalanga Province shows an invasive potential over most of the Olifants and Komati catchments in the northern and central regions of the province. The bioclimatic variable that contributed most to the model performance was mean temperature of the coldest month. Temperature is critical variable that determines suitable environments for the occurrence of rainbow trout (Matthews & Berg, 1997). The area that was predicted as climatically suitable for rainbow trout is known to be among the coldest regions in the province with a low average air temperature of 14°C during winter and an annual average of 22°C. This was reflected in the response curves which showed that the areas that were predicted as suitable for rainbow trout were mainly associated with areas that had cool annual mean temperatures (4–15°C). This is consistent with other studies elsewhere in South Africa that have shown that low temperature is the primary variable that influences the invasions by rainbow trout (Ellender, Weyl, & Swartz, 2011; Rivers-Moore et al., 2019; Shelton et al., 2018).

The results of this study are also consistent with previous assertions that have shown that despite sustained introduction effort, there is still a considerable area-based invasion debt for rainbow trout in some parts of the country (Ellender, Rivers-Moore, Coppinger, Bellingan, & Weyl, 2016; Rivers-Moore et al., 2019). Of these ~3,500 km river length that was predicted to be suitable for rainbow trout in the province, only 35% is currently occupied, and the area-based invasion debt was estimated at 65%. There are several reasons that could account for such a high invasion debt, and these include natural and man-made barriers that impede fish migration, natural thermal barriers that obstruct fish migration, insufficient stocking efforts, protected areas where fish introductions are prohibited, and anthropogenic activities, for example, mining and pollution from urban areas that make some river habitats unsuitable for aquatic fauna. For example, Ellender et al. (2016) found a high invasion debt of trout in the upper Keiskamma catchments in the Eastern Cape and attributed this to limited fish migration due to stream fragmentation by impoundments. In addition, the impoundments also resulted in thermal barriers that influenced fish migrations between river sections. There is a natural thermal gradient between upper river sections and middle to lower sections where river reaches located at high altitude tend to have cooler water temperatures than river reaches located at lower altitude. Trout are cold-water species and are naturally restricted to the upper catchments during summer and migrate downstream during winter when temperature decreases (Ellender et al., 2016). A similar pattern was observed by Shelton et al. (2018) in Cape Fold Ecoregion where high temperatures in summer limited trout density and resulted in more localized occurrences at sites that remained relatively cool, and trout were generally absent from relatively warm sites—indicating seasonal migration between suitable sites.

Natural biogeographical barriers can also influence the potential spread of trout from points of introduction to potential suitable areas by preventing upstream migration of fish. For example, in Blyde River trout were introduced to some sections of the river below the Christmas Pool falls but not in upper river sections above the falls (Engelbrecht & Roux, 1998). The waterfalls act as a natural barrier to upstream fish migration and as a result the river sections above the falls, although suitable for trout are still invasion free. In addition, the upper river section above the falls were also declared a natural heritage conservation area, so human facilitated introductions are prohibited. Similarly, other areas that might be suitable for trout are located in conservation areas, where the introduction of trout is prohibited. The area currently designated as conservation areas in Mpumalanga Province is about 2,500 km^2 in extent and about 12.5% of the area is predicted as suitable for rainbow trout. The conservation area includes upper catchments of several river systems that are designated as fish sanctuaries for endemic river minnows that are threatened by human activities such as alien fish introductions. For example, the catchment of the Treur River is within the Blyde River Canyon Nature Reserve which is designated as a protected area partly because the Treur River is inhabited by the endemic *Enteromius treurensis* Groenewald, 1958 (Treur River barb) that is listed as critically endangered because of alien predatory fish such as rainbow trout, brown trout, and *Micropterus dolomieu* (Lacepède, 1802; smallmouth bass; Roux & Hoffman, 2017).

Anthropogenic activities such as mining can also alter stream habitats, for example, gold mining activities have been implicated in a decline and fragmentation of fish communities in the upper Blyde River catchment (Kleynhans, 1987). Water abstraction is another form of anthropogenic activity that was reported to cause destruction in fish habitats in South Africa, resulting in limited fish distribution in the Cape Floristic Region and the Olifants River system. Water abstraction leads to low river flows in dry and hot summer months limiting the availability of suitable habitats for species such as *Austroglanis barnard* (Skelton, 1981; Barnard's rock catfish) and *Austroglanis gilli* (Barnard, 1943; Clanwilliam rock catfish; Weyl, Finlayson, Impson, Woodford, & Steinkjer, 2014).

There are currently >200 localities with the confirmed occurrence of rainbow trout in South Africa, and this may not represent a true reflection of current occurrence of the species due to the paucity of confirmed occurrence data. This maybe an artefact of low sampling effort rather than low spread rate. This notion is supported by the fact that the government led consultative mapping stakeholder process indicates that trout might occur over a wider range than currently indicated from documented occurrence records. However, this exercise was based on expert opinion and needs to be verified through a formal ground truthing survey. A more accurate spread rate estimate could be given with verified survey records that can be used to predict an informed spread debt over a specific time frame.

4.1 Climate change

The extent of the suitable area for rainbow trout in Mpumalanga Province varied under different climate change scenarios where it was projected to decrease under RCP 4.5 scenarios and increase under the RCP 8.5 scenarios. The significant shifts in the extent of area suitable for rainbow trout under the two scenarios were mainly attributed to changes in isothermality and the mean temperature of the coldest quarter. Isothermality is a measure of how diurnal temperature range fluctuates relative to annual temperature range, and there was a decline in the area predicted as suitable under the RCP 4.5 scenarios when seasonality is projected to be high. Other studies have also predicted that rainbow trout distribution may be influenced by larger temperature fluctuations within a month relative to the year (Ellender et al., 2016; Rivers-Moore et al., 2019; Santiago et al., 2016; Shelton et al., 2018). The increase in suitable area under the RCP 8.5 scenarios was unexpected and was largely due to a projected increase in the minimum temperatures from 11 to 15°C that resulted in a large proportion of the study area that occurs at lower altitudes and experiences warmer minimum water temperatures being predicted as suitable. We take cognizance that other variables (e.g., thermal thresholds) influence rainbow trout distributions and the larger proportion of area predicted as suitable for rainbow trout under a warming climate might be a modeling artefact that might be resolved by including mechanistic variables in the models (e.g., Evans, Diamond, & Kelly, 2015; Kearney & Porter, 2009; Rivers-Moore et al., 2019).

4.2 Management implications

The management of rainbow trout in South Africa is contentious because of different value systems between stakeholders and conservation authorities (Woodford et al., 2016; Zengeya et al., 2017). Part of the management initiatives for rainbow trout includes managing it by area where utilization is allowed in areas where it has established and in areas where it has been historically utilized for stocking (Ellender et al., 2014; Woodford et al., 2017). This management approach requires accurate occurrence data to work effectively and reduce contestations around known trout distribution. The current records available on trout distribution in South Africa are limited and were mostly generated through stakeholder–government initiatives using expert opinion to map areas of occurrence. These records, however, have drawbacks that compromise their accuracy because they have not been verified, and highlight the need for regular monitoring programs to generate long-term distribution data for alien species in freshwater systems around the country. The findings of this study compliment this stakeholder–government initiative to map the distribution of trout by projecting potential suitable areas of occurrence and how the distribution is likely to be affected by climate change. The results indicated that rainbow trout only occupies a fraction of the current potential suitable river length in Mpumalanga Province which implies that there is a high area-based invasion debt and there is a risk that it may spread further. The large unoccupied projected suitable area may also imply that the range of current distribution of trout in Mpumalanga Province may be wider than indicated, given the lack of ground truthing for verification of occurrence. This is especially worrying given that several studies have shown that trout can have a significant effect on fish communities and that there is a need to prevent human-facilitated introductions in biodiversity sensitive areas such as mountain headwater streams that are inhabited by endemic and range restricted minnows (e.g., Maimela, Chimimba, & Zengeya, 2021; Weyl et al., 2020). It is also likely that if there is a range shift in suitable habitats for trout due to climate change, new conflicts might arise due to the need to exploit suitable areas that are not currently designated as trout areas (Rivers-Moore et al., 2019).

The major findings of this study are that there is a high invasion debt for trout in river systems in Mpumalanga Province and the areas predicted as suitable for trout in the province might not be static and are likely to shift with climate change. The estimates are however compounded by a lack of verified occurrence data and should be recognized as a high estimate that can be improved upon through the establishment of regular monitoring to accurately document trout occurrence in the country.

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