

Niche shift and resource supplementation facilitate an amphibian range expansion

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Abstract

Aim: To determine whether recent range expansion of small-bodied arboreal frogs, *Hyperolius marmoratus* Rapp, is accompanied by changes in species–environment relationships and whether its historical range was constrained by climate, availability of water bodies or topographic variables. We test if artificial water bodies in the novel range have facilitated niche shift by increasing available habitats for frog establishment.

Location: Western Cape Province, South Africa, with reference to the broader species range in southeastern Africa.

Methods: We build species distribution models using occurrence data from the historical and novel ranges and reciprocally project them to highlight areas of putative niche change. We test for niche shift through ordination-based approaches to disentangle how species–environment relationships may have altered and whether climate or landscape features (artificial water bodies and topography) are more strongly associated with the identified change. We further decompose niche change into areas of expansion and unfilling to quantify niche shift and describe potential future spread.

Results: We observed niche expansion into novel environmental space, with 21% of niche space in the invaded range composed of environments that were not occupied in the native range. We also observed 16% niche unfilling, signifying range disequilibrium and potential for further spread. Mean annual precipitation and proximity to water bodies were more influential in models constructed in the novel range than in historical or combined range models, suggesting that presence of artificial water bodies in the landscape ameliorates novel range conditions. Together, these metrics suggest that range expansion may be ongoing based on climate and water body availability.

Main conclusions: Our analyses identify a realised niche shift that has allowed painted reed frogs to occupy drier and more thermally variable habitats in their novel (invaded) range. This shift may be mediated by artificial water bodies that provide additional buffered habitats, a key resource supplement for these small-bodied tropical frogs.

KEYWORDS

invaded range, invasive species, niche model, species distribution model

1 | INTRODUCTION

Determining which factors influence the spread and distribution of invasive species can facilitate a range of important outcomes, from describing large-scale patterns of species distributions, to informing local management and control practices (Sax et al., 2007). A useful framework for understanding the limits of distributions and helping to predict future invasion patterns is the concept of the niche. While the niche can be interpreted and analysed in a number of ways, the realised niche, that is the portion of the fundamental niche actually occupied by the species due to limits set by both biotic and abiotic interactions, and dispersal ability (Wiens & Graham, 2005), is useful for investigating broad-scale distribution patterns. The realised niche can be approximated by comparing species–environment relationships across geographical ranges (Broennimann et al., 2012; Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). A challenge when analysing the realised niche in this manner is that additional processes, including adaptation, may facilitate species range expansion into environments that they were previously not able to occupy. This is termed “niche shift”, and identifying signatures of this process is an important area of invasion biology research (Higgins, Richardson, Cowling, & Trinder-Smith, 1999; Hill, Chown, & Hoffmann, 2013; Hill, Gallardo, & Terblanche, 2017).

Species distribution models (SDMs) are widely used to correlate observed distributions with environmental covariates, hence constructing an approximation of the realised niche (Guisan & Thuiller, 2005). The ability of species distribution models to describe the realised niche and accurately predict distributions of invasive populations relies on assumptions of distribution equilibrium (Early & Sax, 2014; Elith & Leathwick, 2009) and niche conservatism (Pearman, Guisan, Broennimann, & Randin, 2007; Wiens & Graham, 2005). When these assumptions are violated, niche models may under- or overpredict range limits, making the identification of niche shift more difficult (see Broennimann & Guisan, 2008). Methods that allow for decomposing niche change into centroid shifts, degree of overlap, and amounts of expansion and unfilling (Guisan et al., 2014) facilitate the quantification of niche shifts and improve the formulation of hypotheses surrounding the mechanisms underlying invasion success such as rapid evolution (Lee, 2002), phenotypic plasticity (Kolbe, VanMiddlesworth, Losin, Dappen, & Losos, 2012; Hill et al., 2013; McCann, Greenlees, Newell, & Shine, 2014) or enemy release (Sax et al., 2007). While climatic predictors are chiefly employed in niche modelling, consideration of human activities and land use is also important for generating hypotheses about the drivers of change (Kearney, 2006) and accounting for temporal changes in species distributions (Rapacciuolo et al., 2012).

Understanding how climate and land use work together to influence niche changes should help to identify undetected areas of occupancy of species that are already introduced (Gallardo, Zieritz, & Aldridge, 2015) and aid conservation and management decisions. Such studies can lead to better targeting of control measures in areas where suitable climate and sites of likely introduction coincide

(Peterson, 2003) and allow adaptive management based on initial management outcomes (Muirhead et al., 2006).

The Western Cape Province of South Africa is poor in natural water bodies, particularly larger lentic systems (Shaw, 1988), but artificial impoundments such as farm dams and irrigation canals are common on agricultural land, adding to the freshwater aquatic habitat available in the landscape. Artificial water bodies make up the vast majority (91%) of the water bodies in the Western Cape (Davies, Clusella-Trullas, Hui, & McGeoch, 2013) and provide additional habitat for extralimital and indigenous birds (Froneman, Mangnall, Little, & Crowe, 2001), amphibians (Hazell, Hero, Lindenmayer, & Cunningham, 2004) and invertebrates (Brainwood & Burgin, 2009). In agricultural and peri-urban landscapes of South Africa, they are instrumental in the invasion of painted reed frogs (Davies et al., 2013) and guttural toads (Vimercati, Hui, Davies, & Measey, 2017). Okes, Hockey, and Cumming (2008) found that most water birds that expanded their ranges did so towards the west of South Africa, and suggested that these species were preadapted to using artificial impoundments, although they also made use of a range of natural wetland types. Hockey et al. (2011) found that 13% of 283 South African bird species had expanded their ranges westwards in opposition to climate change model expectations; these were mainly habitat generalists and made use of human-modified habitats, pointing to the need to incorporate human-modified landscape elements in models of range change. In addition to resource supplementation, farm dams may also facilitate the range expansion process by providing stepping stones, corridors (Lobos & Measey, 2002 for *Xenopus laevis*) or networks (Woodford, Hui, Richardson, & Weyl, 2013 for freshwater fish) which increase propagule transfer through the landscape.

The painted reed frog is a member of the Old World tree frogs, and the genus *Hyperolius*, the largest genus of African frogs. The published distribution (Bishop, 2004; Passmore & Carruthers, 1995) is across southeastern Africa, including southern Tanzania, Malawi, Mozambique, Zimbabwe, Zambia, Swaziland and the northern and eastern parts of South Africa (Bishop, 2004; Channing, 2001; Poynton & Broadley, 1987; Figure 1). Starting in about 1997, the species underwent a rapid, long distance range expansion into the southwestern parts of South Africa, probably linked to the transport of nursery plants and garden equipment (Bishop, 2004). Between 1998 and 2009, the frogs spread a distance of approximately 400 km in a westerly direction and established breeding populations around Cape Town and in inland areas of the Western Cape Province (Davies et al., 2013; Figure 1). Western Cape populations exhibit a mixture of genotypes typical of populations from the far northern and eastern parts of South Africa (Tolley, Davies, & Chown, 2008). While the historical range of the painted reed frog has a tropical to subtropical climate with summer rainfall, the novel range has a temperate, Mediterranean-type climate with a bimodal or winter rainfall pattern (Bishop, 2004; Davies et al., 2013; Tolley et al., 2008). Painted reed frogs have broad thermal tolerance (~0 to 40°C; Davies, McGeoch, & Clusella-Trullas, 2015), allowing them to occupy a range of climatically variable habitats in the subtropical regions of southern Africa. However, it is possible that autonomous dispersal

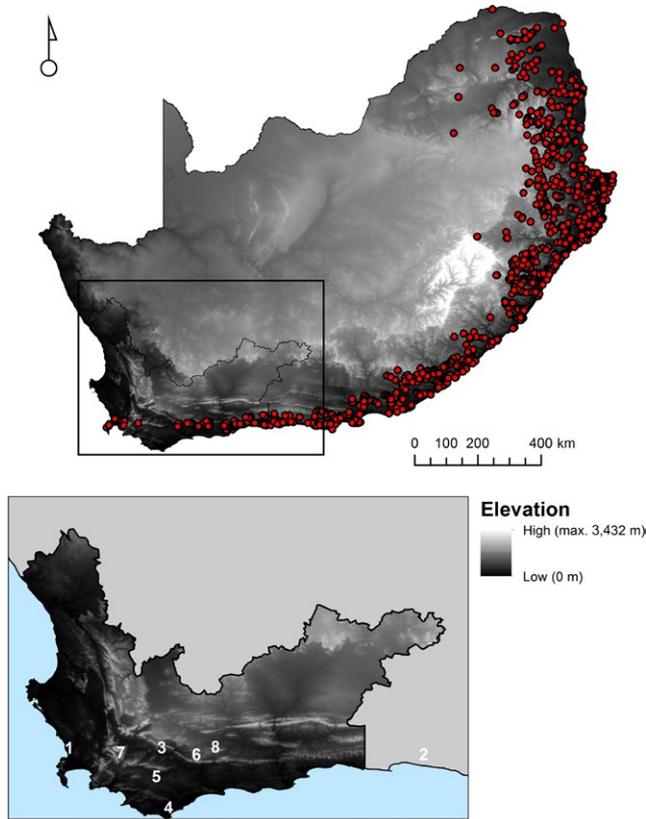


FIGURE 1 Regional range of the painted reed frog, *Hyperolius marmoratus* Rapp, prior to range expansion (main panel). Red dots are presence data used in the models. Inset shows the novel range; white numbers indicate locations mentioned in the text: 1 Cape Town/Cape Peninsula, 2 Tsitsikamma Forest, 3 Cape Fold mountain ranges, 4 Cape Agulhas, 5 Agulhas Plain, 6 Swellendam, 7 Villiersdorp, 8 Barrydale [Colour figure can be viewed at wileyonlinelibrary.com]

between neighbouring water bodies also played a role in the range expansion (Tolley et al., 2008; Davies et al., 2013). Understanding the non-climatic drivers of range expansion in the painted reed frog may allow potential management actions for *Hyperolius marmoratus* to be targeted more realistically within urban or agricultural areas and may inform local management strategies for other urban exploiters such as the guttural toad, *Sclerophrys gutturalis* (Measey et al., 2014; Vimercati et al., 2017).

In this study, we test for niche change in the painted reed frog (*H. marmoratus* Rapp) across its historical and novel (invaded) ranges in South Africa, to discover whether the species niche in the historical range is constrained by climate or by other environmental characteristics of the historical range. First, we build SDMs using comprehensive occurrence data for the historical and novel ranges of the species within South Africa and apply them in a reciprocal framework (e.g., Broennimann & Guisan, 2008; Fitzpatrick, Weltzin, Sanders, & Dunn, 2007; Hill, Hoffmann, Macfadyen, Umina, & Elith, 2012). We use these SDMs to examine whether the species had overcome its climatic limits during invasion and identify particular areas of niche change. We then decompose the putative niche changes using the centroid shift, overlap, unfilling and expansion

(COUE) scheme of Guisan et al. (2014) to determine whether there have been any changes in niche dimensions during invasion and whether the range expansion has been limited or facilitated by human activities and land use. We particularly focus on topography and the availability of water bodies and rivers as potential drivers of range expansion as these have been shown to influence the accessibility and availability of suitable habitat for *H. marmoratus* (Davies et al., 2013).

2 | METHODS

2.1 | Occurrence data

Painted reed frog occurrence data were sourced from existing databases covering South Africa, Lesotho and Swaziland: the South African Frog Atlas Project (SAFAP; Minter et al., 2004; records from 1905 to 2003), the CapeNature State of Biodiversity database (CNSOB; Turner, 2006; records from 1997 to 2006) and systematic and opportunistic sampling across the novel range (Davies et al., 2013; records from 2006 to 2010). In both the SAFAP and CNSOB datasets, records were only retained if they were reported at a resolution of 1 s (0.000278 decimal degrees). Available records from Zimbabwe, Mozambique, Zambia and Malawi were excluded from our analysis due to the risk of misidentification and confusion with other members of the *Hyperolius viridiflavus* complex that occur in the northern part of the species range (Schlötter, 1971, 1999; Wicczorek, Drewes, & Channing, 2001). *Hyperolius marmoratus sensu stricto* within South Africa, Lesotho and Swaziland was regarded as reliable and formed the focus of our models and analyses (Bishop, 2004; Channing, 2001; Poynton & Broadley, 1987). Within the study domain, the novel range was defined as the portion of the Western Cape Province west of 23°E longitude, while the historical range covered the remainder of South Africa, that is the area north and east of Tsitsikamma forest, the documented historical boundary of the species range (Channing, 2001; Passmore & Carruthers, 1995; Figure 1). The novel and historical occurrence datasets did not overlap and there was clear spatial and temporal separation between the historical distribution ("historical range") and the range expansion area ("novel range") (Davies et al., 2013). This provided two spatially and temporally distinct occurrence datasets (Table 1). In total, 151 verified records of *H. marmoratus* occurrence were available from the novel range and 1,221 records from the historical range.

2.2 | Environmental predictors

Climatic variables were selected on the basis of known physiological tolerance, ecological relationships and natural history (Wiens & Graham, 2005). We used functionally-relevant proximal variables that were likely to limit painted reed frog distribution: evaporative potential in the driest month of the year in the novel range (January) (Chiew & McMahon, 1992; Davies et al., 2013), degree days for

TABLE 1 Summary of data sources and numbers of records used in niche models of *Hyperolius marmoratus* Rapp

	Historical range	Novel range
Years	1908–2003	1997–2010
Sources	SAFAP	SAFAP, CNSOB, authors' surveys
No. of presence records	1,221	151
No. of target group absences	1,738	28
No. of random pseudo-absences	834	166

Data sources: South African Frog Atlas Project (SAFAP; Minter et al., 2004), CapeNature State of Biodiversity Database (CNSOB, Turner, 2006) and authors' surveys (Davies et al., 2013).

the three peak winter months (Davies et al., 2013), and mean annual precipitation, a broad-scale range limiter for many amphibians (Wells, 2007). A further climatic variable, daily temperature range in summer, was introduced as a measure of metabolic challenge experienced by frogs during the breeding season. These climate data were extracted from the South African Atlas of Agrohydrology and Climatology at 1' × 1' resolution (interpolated raster data; Schulze, Maharaj, Lynch, Howe, & Melvil-Thompson, 1997). The predictors were weakly cross-correlated (Spearman's r values < 0.355), except diurnal temperature range in the breeding season × degree days in winter ($r = -0.637$) and diurnal temperature range in the breeding season × mean annual precipitation ($r = -0.646$) which were moderately correlated.

In addition to climate, the availability of water bodies and riparian corridors provide sheltered microhabitats to amphibians, as well as foraging areas and routes for dispersal. Spatial layers describing artificial water bodies (captured at 30 m resolution) and riparian corridors (rivers; captured at 1:500,000 scale) were obtained from the South African National Freshwater Ecosystem Priority Areas database (NFEPA; Nel et al., 2011). These data were then transformed into gridded data at the same resolution as the climate layers, with cell values being the proximity to the nearest water body or river spatial feature measured using QGIS (Quantum GIS Development Team, Open Source Geospatial Foundation Project 2010 with MMQGIS plugin from <http://michaelminn.com/linux/mmqgis/>, accessed 10 July 2014). Artificial water bodies were extracted from the water body layer (i.e., natural water bodies were excluded). Previous habitat modelling (Davies et al., 2013) had suggested that mountainous and rugged areas may be inaccessible to painted reed frogs, so we also examined the effect of topography in the models by including the "terrain morphology" variable from Schulze et al. (1997), which represents a composition of slope, slope form, relief, drainage density and drainage frequency devised by Kruger (1983). High terrain morphology values denote high terrain rugosity, steep slopes and dissected landscapes; values are assigned in six classes (A–F) and 30 subclasses (subclasses 1–30) ranging from plains with low relief (A; subclasses 1–4) to closed hills and mountains with moderate and

high relief (E; subclasses 23–29) and tablelands with moderate and high relief (F; subclass 30).

Prior to constructing distribution models and identifying putative changes in species–climate relationships, we defined a geographical background area using the ecoregions dataset defined by Olson et al. (2001), as this biogeographical resolution matched the scale of the invasion. We created geographical masks for each range based on the occupied ecoregions (unique ecoregions that held an occurrence record; Hill et al., 2017; Mateo, Croat, Felicísimo, & Muñoz, 2010). The rationale for this approach was that we wished to restrict model training to areas that fell within suitable potential habitat, but may have not have been colonised for a number of reasons.

Within the defined background, we identified localities where other nocturnal, summer-breeding frog species were recorded in the SAFAP database (52 species, Supporting Information Appendix S1; Minter et al., 2004), during the core painted reed frog breeding months of October to February, but where *H. marmoratus* was not recorded, and used these records as target group absences ($n = 1,766$ records; see Table 1). Considering the conspicuous nature of *H. marmoratus* (loud call >100 dB, large breeding choruses and extended reproductive season, Du Preez & Carruthers, 2009), we assumed that these records closely simulated actual absence data (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Mateo et al., 2010) as records were from sites where expert search effort had been made for anurans. Initial distribution models (see Section 2.3 below) were run with this absence dataset, and then, to increase the discrimination and transferability of the models and ensure that the area available to painted reed frogs was accurately represented, we added 1,000 randomly-generated pseudo-absences across the geographical limits defined by the occupied ecoregions (Olson et al., 2001). Therefore, the final pseudo-absence dataset for our models was a combination of biological reasoning (target group absences) and randomly-selected points within potentially suitable habitat and yielded an absence dataset ($n = 2,766$) that fully represented the area available to the species (see Parida, Hoffmann, & Hill, 2015).

2.3 | Modelling approach

To construct SDMs, we used boosted regression trees (BRTs; Elith, Leathwick, & Hastie, 2008) using the "dismo" package (Hijmans, Phillips, Leathwick, & Elith, 2013) in R (R Development Core Team 2012). Boosted regression trees employ a machine learning approach to refine an initial postulated relationship between the response variable (species presence–absence) and the predictors (Elith et al., 2008). Boosted regression trees allow for robust modelling of nonlinear relationships and interactions between highly correlated predictors and permit the correlations to be examined explicitly (Elith et al., 2008), making them highly suitable for species distribution modelling purposes. We constructed BRTs for three different geographical extents and datasets: training data from the historical range only ("historical model"), from the novel range only ("novel model") and from both historical and novel ranges together ("all-SA model") using all available predictors. Models were constructed

using climate predictors only and then using the full predictor set. We then used the `gbm.step` function in “`dismo`” (Hijmans et al., 2013) to build the final models with a learning rate of 0.005, which was low enough to achieve over 1,000 trees, thereby optimising the accuracy of the models and their predictive ability (Elith et al., 2008). Tenfold cross-validation and a bag fraction of 0.5 were used to introduce stochasticity into the model-building process.

Models were evaluated using area under the curve (AUC), sensitivity, specificity and true skill statistic calculated in the “`dismo`” and “`PresenceAbsence`” packages in R (Freeman & Moisen, 2008a,b; Hijmans et al., 2013). Model outcomes were assessed in the light of available biological information, including physiology, thermal tolerance and natural history (Rödder, Schmidtlein, Veith, & Lötters, 2009). The final models that had been trained in the novel or historical range were then reciprocally projected to determine whether *H. marmoratus* occupies similar habitats across ranges in South Africa and to identify changes in variable importance between ranges (Fitzpatrick et al., 2007; Hill et al., 2012). To measure niche overlap between pairs of models projected onto the same geographical space, we used Schoener's *D* (Schoener, 1974) and the niche similarity test in R package “`ecospat`” (Di Cola, Broennimann, Petitpierre, Breiner, D'Amen, et al. 2017).

2.4 | Niche overlap in environmental space

To quantify potential shifts in the niche of *H. marmoratus*, we used the Centroid, Overlap, Unfilling, Expansion (COUE) framework of Guisan et al. (2014) to decompose niche changes into centroid shifts, degree of overlap and amounts of unfilling and expansion. We first conducted a principal components analysis (PCA) across both historical and invaded niches. Then, for calculation of the niche shift metrics (stability, expansion, unfilling), using the R package “`ecospat`”, we rescaled the first two PCA axes to a resolution (extent) of 100 × 100 cells (Broennimann et al., 2012; Petitpierre et al., 2012) to reduce the effects of geographical extent, sampling bias and missing data. This rescaling process allows for different niches to be compared directly, as it reduces the effects of sampling bias and missing data within and between ranges (Broennimann et al., 2012). The species occurrence points were then projected onto the respective niche surfaces, and the density of occurrence points for each grid cell was calculated using kernel smoothing, which allows the density (as opposed to frequency) of occurrences to be compared, so that occupied environmental space is better represented (Broennimann et al., 2012). These two-dimensional representations of the niche maximise environmental differences and allow for any differences in range size to be largely discounted. This analysis allows us to distinguish between true niche shift and apparent shift due to occupation of environments that were not available in the historical range. The native and invaded niche surfaces were overlaid and the niche metrics were calculated at the intersection of the two surfaces within the total niche space available (Guisan et al., 2014; Petitpierre et al., 2012) as follows: (a) niche expansion describes environments which are

available in both native and invaded niches, but only occupied in the invaded niche (Guisan et al., 2014). (b) niche stability refers to those environments which are occupied in both native and invaded niches. (c) niche unfilling describes environmental space in the native range that is available, but not yet exploited, in the invaded range. We ran the PCA first on the four climate predictors only and then used the full variable set (seven variables) to examine the effect of adding topography and proximity to water bodies.

2.5 | Environmental similarity across the ranges

Niche models can be sensitive to the availability and distribution of environmental gradients in the study area, and projecting models outside the training area may result in extrapolation beyond the reference range of one or more environmental predictors (Mandle et al., 2010; Parida et al., 2015). Such predictions can be unreliable, so we used multivariate environmental similarity surfaces (MESS; Elith, Kearney, & Phillips, 2010; Elith et al., 2011) in “`dismo`” to measure environmental similarity across each range and permit the identification of non-analogue environments that may affect the models (Guisan et al., 2014). In a separate analysis, we also compared the mean distance between water bodies in the historical and novel ranges through determining the nearest neighbour. We then compared the mean nearest neighbour distances between ranges using ANOVA.

3 | RESULTS

3.1 | Species distribution models: best predictors and model performance

Mean annual precipitation was the most influential variable in the novel range and diurnal temperature range was most influential in the historical range (Table 2). The models displayed consistently high AUC values (0.907–0.999) and correctly identified most presences (high specificity) and absences (high sensitivity; see Table 3). True skill statistic was ≥ 0.827 for all models, indicating reasonably accurate predictions of current distributions by the novel, historical and all-SA models (Table 3). Reciprocal projections of the novel, historical and all-SA models showed that the models had high predictive ability in the reciprocal ranges (0.763–0.987). Variable response curves are shown in Supporting Information Appendix S4.

3.2 | Areas of concordance

Models trained with all-SA data gave similar predictions, probably because of the large geographical overlap of the two training areas (approx. 90%). Areas of concordance between all of the models were along the east coast and northeastern inland parts of the country (high suitability); the high elevation and generally arid central part of the country (low suitability); and the mountainous central parts of the Western Cape Province (Swellendam to Villiersdorp) (low

suitability). None of the models predicted high suitability in the very high-lying, central plateau.

3.3 | Predictions for the novel range

Predictions of the historical model in the novel range correctly show a high probability of occurrence in the east of the region and in the lowlands of the southwestern Cape, and that the southernmost area, the Agulhas Plain, has not been colonised. The model trained in the novel range showed more limited areas of suitable habitat (Figure 2b), compared with the other two models (Figure 2a,c) which predicted larger areas of suitable habitat across the Western Cape. The areas of suitable habitat predicted by the models generally fell into three main parts: (i) the mesic eastern part of the novel range, near its boundary with the historical range, with a narrow extension westward along the Cape Fold mountain foothills towards Swellendam (see Figure 1 for locations of places mentioned); (ii) the western part of the province from the southernmost tip of South Africa (Cape Agulhas) to the Cape Peninsula and northwards into the Cape Fold mountains; and (iii) the Cape Peninsula in the extreme

southwest. This latter area is highly mountainous, flanked by a narrow coastal belt and thus provides little accessible habitat and few wetlands.

The historical and all-SA models made similar predictions when projected onto the novel range, but differed in the extent of suitable habitat (Figure 2b,c). Both models predicted that the riparian corridors of the largest rivers, which mostly fall in the eastern part of the novel range, were suitable. Some suitable areas were predicted to the north of Cape Town, but these are not in fact occupied by painted reed frogs.

3.4 | Predictions for the rest of South Africa

The model trained in the novel range correctly predicted occurrence of painted reed frogs across large areas of the historical range in northern and eastern South Africa. The novel model also predicted a much broader area of occurrence than did the historical or all-SA models (Figure 2b), suggesting that parts of the interior mountain ranges (e.g., the Maloti-Drakensberg mountain foothills) may be suitable habitat for painted reed frogs. However, the model predictions in this area should be interpreted with caution because some of these parts of northeastern South Africa are extrapolations outside the training range of the models (see MESS maps in Supporting Information Appendix S2).

3.5 | Niche overlap and niche shift

The COUE analysis revealed a shift in the climate niche centroid towards areas with higher evaporation and thermal variability when both the climate only and full predictor sets were used (Figure 3). Figure 3b shows the interplay between humidity/aridity, temperature and temperature variability (PC axis 1) and habitat availability/quality (PC axis 2) in determining the niche of *H. marmoratus* (see Supporting Information Appendix S3 for predictor loadings on the PC axes). The analysis using the full predictor set of seven variables showed that 21% of the painted reed frog's climate niche is within novel climate space, reflecting niche expansion. However, some suitable areas in the novel range are not occupied (16% unfilling when calculated using only the common niche space). This indicates that there is disequilibrium or ongoing range unfilling in the novel range. The niche also shows 79% stability, indicating that the majority of the niche space is common between the historical and novel ranges (see Table 4).

TABLE 2 Relative influence of predictors in the boosted regression tree (BRT) models of *Hyperolius marmoratus* ranges

Predictors	Relative influence in models (%)		
	Historical	Novel	All-SA
Evaporation in the driest month	12.6	11.3	16.1
Diurnal temp. range in breeding season	27.5	22.3	22.8
Degree days in winter	23.5	10.2	22.6
Mean annual precipitation	19.4	31.5	19.6
Topography	5.1	8.6	7.2
Distance to rivers	3.1	4.4	3.1
Distance to artificial water bodies	8.8	11.8	9.6

Notes. Values are variable contributions to models. "Historical", "novel" and "all-SA" denote the range areas used to train the models. All variables were retained after model simplification based on change in deviance when the predictor was removed (gbm.simplify function in "dismo" package of R; Hijmans et al., 2013).

TABLE 3 Performance of reciprocal niche models (boosted regression trees; BRTs) of *Hyperolius marmoratus* trained in the historical, novel or all-SA ranges

Model	Threshold	AUC _{train}	Sensitivity	Specificity	TSS
Historical	0.58	0.973 ± 0.003	0.907 ± 0.009	0.920 ± 0.009	0.827
Novel	0.80	0.999 ± 0.000	0.980 ± 0.012	1 ± 0	0.980
All-SA	0.57	0.976 ± 0.003	0.920 ± 0.008	0.914 ± 0.009	0.834

Notes. Models were built using a learning rate of 0.005, 10-fold cross-validation and a bag fraction of 0.5). Threshold = optimal threshold that maximises sensitivity + specificity; AUC_{train} = AUC of the model in the training range; values are mean ± SD; TSS = true skill statistic.

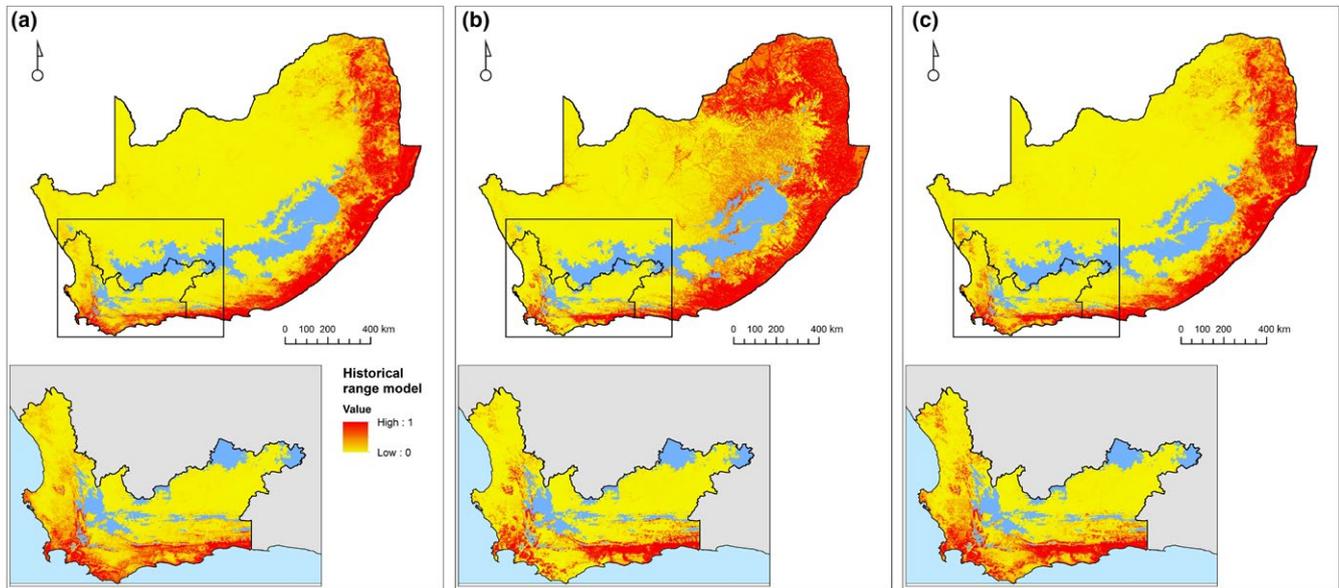


FIGURE 2 Model predictions from boosted regression tree models using the full predictor set. Models trained in the historical range (a), novel range (b) and all-SA range (c) show the predictions of probability of occurrence where red is high and yellow is low probability. Blue areas are those with no model prediction due to lack of occurrence and background data [Colour figure can be viewed at wileyonlinelibrary.com]

When climate predictors alone were used, niche overlap between the historical and novel niches was relatively high (Schoener's $D = 0.43$) and the niche similarity test (Warren et al., 2008) showed that the historical range and the novel niches were more similar than expected by chance (Table 4). When we included variables describing topography and distance to water bodies, however, niche similarity and niche overlap between the historical and novel ranges were reduced (Schoener's $D = 0.24$; Table 4). The hypothesis of niche similarity between the historical and novel niches was rejected when only climate predictors were used (Table 4).

3.6 | Non-analogue environments

The MESS analysis showed some areas of the historical range lying outside the range of predictor values used to train the novel model (see Supporting Information Appendix S2). However, many of these also fell outside the model background. Within the model background, the northeastern part of the historical range has intermediate environmental similarity values to the novel range, driven by differences in evaporation in January, reflecting the distinct rainfall seasonality of the historical and novel ranges. In contrast, predictor values in the novel range are a subset of those found in the historical range, with the exception of the highest peaks of the Cape Fold Mountains which are exceptionally cool and wet for South Africa. Because of the generally low level of climate dissimilarity within the model domain (see Supporting Information Appendix S2), we did not exclude non-analogue areas from the models but took them into account in interpreting model performance and predictions.

The nearest neighbour analysis of water bodies across the historical and novel ranges showed that water bodies were more closely

spaced (i.e., more densely distributed) in the novel range (mean nearest neighbour distance \pm SD, 326.8 ± 484.9 m) than in the historical range (455.6 ± 611.3 m; ANOVA: $F_{1,431034} = 2620$, $p < 0.001$).

4 | DISCUSSION

Using reciprocal modelling of the historical and novel ranges of the painted reed frog permits testing of ideas surrounding niche shifts and relates broad-scale patterns back to the life history of the species (Hill et al., 2012). The range expansion of *H. marmoratus* from its historical range in the northern and eastern coastal regions of South Africa to the Mediterranean ecosystems of the southern and southwestern Cape reflects a shift into a region that is in general drier and more thermally variable than the historical range. Our modelling revealed that diurnal temperature range in summer is an important variable influencing painted reed frog distributions in the historical range, suggesting that the metabolic challenge posed by diurnal temperature variation may reduce the breeding success and possibly survival of this small-bodied amphibian.

Consistent with this observation, our models showed that environmental variables relating to water availability (mean annual precipitation and distance to rivers and artificial water bodies) were more important in the novel range than they were in the historical range or across the combined historical and novel ranges (see Table 2). The availability of water in the form of rainfall and standing and flowing water bodies in the landscape, along with other potential drivers such as propagule pressure, could be a driver of expansion into climate space that was previously inaccessible. Similar trends have emerged for other taxa such as Odonata in Britain (Hickling,

Roy, Hill, & Thomas, 2005), water birds in South Africa (Okes et al., 2008), and a highly invasive amphibian in Australia (Letnic, Webb, Jessop, Florance, & Dempster, 2014; Tingley, Vallinoto, Sequeira, & Kearney, 2014). Unoccupied niche space (indicated by niche unfilling) increased when the full set of predictors was used. The lower niche overlap with the full predictor set is likely due to increased unfilling (16% compared to 8%). This unfilled niche space in the novel range may point to future expansion (range disequilibrium), or may be inaccessible because of topographic barriers or lack of aquatic habitat. This is consistent with the observed large gaps in the distribution of the painted reed frog in mountainous areas of the novel range (Davies et al., 2013).

Areas in which our models did not provide congruence suggest that the model calibrated in the historical range predicted painted reed frog occurrence in most parts of the southernmost region of south Africa, for example the Agulhas Plain (see Figures 1 and 2), while the novel range models did not. Painted reed frogs may be excluded from this large (c. 1,500 km²) coastal plain by the lack of suitable water bodies there. This could be due to high salinity levels resulting from the underlying marine-derived sediments and strong inundation and drying cycles (Russell & Impson, 2006); alternatively, the area may in fact be suitable, but has not been colonised because of dispersal or other limitations. Interestingly, all the models predicted some suitable habitat for painted reed frogs on the inland

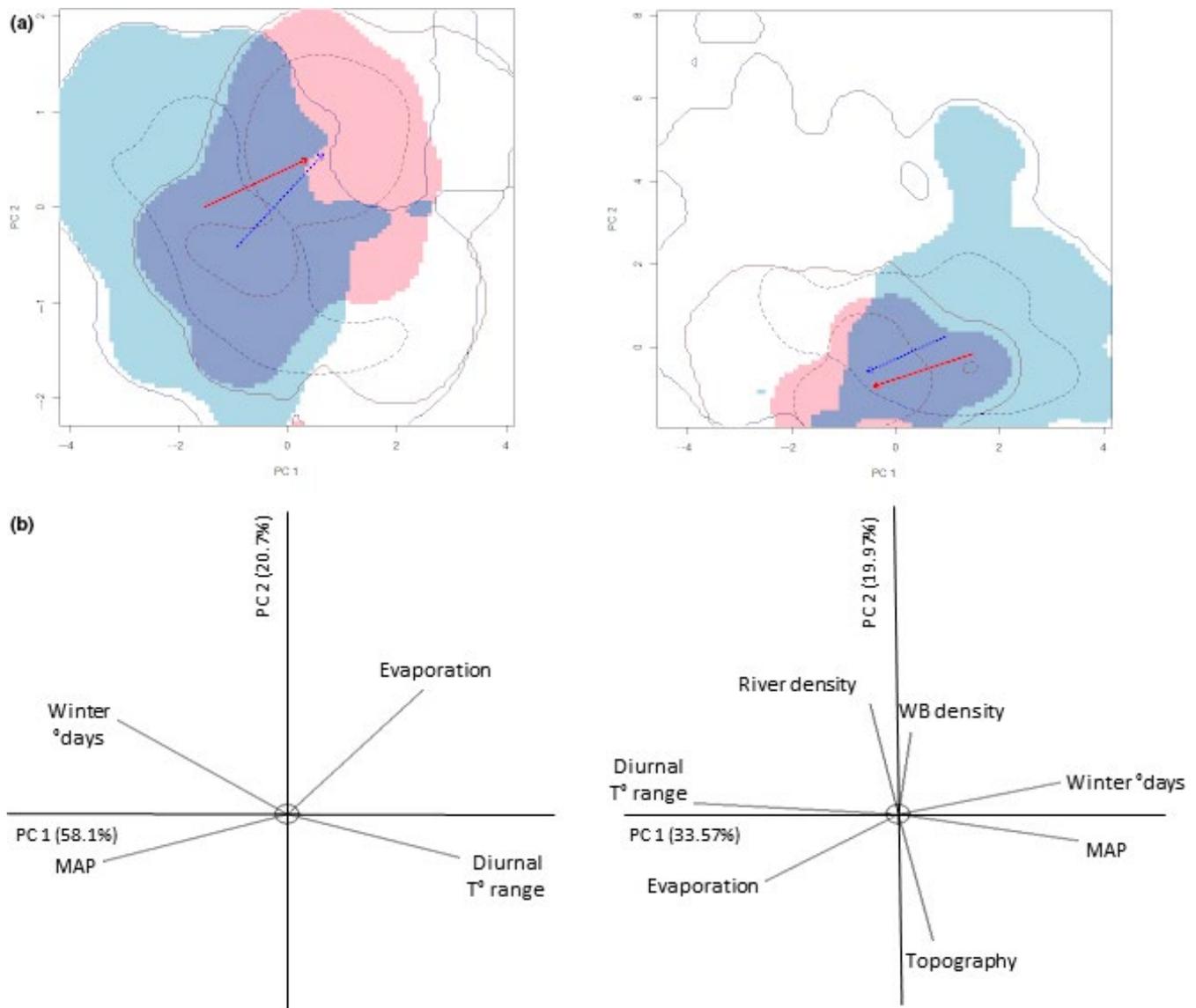


FIGURE 3 *Hyperolius marmoratus* Rapp niche shift in environmental space (a), derived from principal components analysis on the climate predictors (left) and the full predictor set (right). The blue shaded area is the unoccupied niche; pink is the expansion area; and purple-grey is the stable niche area. Bounding lines (blue=historical range, red=novel range) show 100% of available climates (solid lines) and the 50% most frequent available climates (dashed lines). Arrows show centroid shift between the historical and novel ranges (red arrow = available climates, blue arrow = occupied climates). Correlation circle (b) shows the contribution of climate predictors (left) and all predictors (right) to the PCA axes. Loadings on the axes are shown in Supporting Information Appendix S3 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Niche metrics derived from principal components analysis using the COUE approach (Guisan et al., 2014)

	Climate predictors only	Full predictor set
Niche overlap (Schoener's D)	0.43	0.244
Niche similarity (hist. → novel)	$p = 0.010$	$p = 0.109$
Niche similarity (novel → hist.)	$p = 0.010$	$p = 0.129$
Niche expansion	20%	21%
Niche stability	79%	79%
Niche unfilling (using common environmental space only)	8%	16%

plateau of South Africa (see Figure 2), in locations where only isolated instances of painted reed frog presence have been recorded to date (although the extent of this inland predicted range was much higher in the novel model). This implies that further range expansion in inland areas of the historical range may be possible in future.

As the SDMs in this study approximate the realised niche, they cannot explicitly determine the effects of biotic interactions, dispersal barriers or adaptation during the invasion process (see Kearney, 2006). Beyond the presence of specific land use features such as water bodies, interactions, barriers or adaptive processes may lead to a broader realised niche in the novel range than in the historical range (Guisan et al., 2014). The observed shift in niche for *H. marmoratus* may also be due to fewer or weaker biotic interactions in the novel range. For example, Tingley et al. (2014) found that the niche of *Rhinella marina* (the cane or marine toad) was unfilled in the native range because of the presence of a congeneric species, *R. schneideri* (rococo or Schneider's toad), with which it shares a stable hybrid zone, illustrating the role of interspecific interactions in structuring invasive species ranges. For *H. marmoratus*, competitive release may be important as there is only one co-occurring *Hyperolius* species in the novel range (*H. horstockii*, arum lily frog), compared with eight in the historical range.

Poynton & Broadley (1987) suggested that the absence of tropical frog species in the southwestern Cape at that time was due to slow post-Pleistocene dispersal rates. Our findings suggest that increased availability of artificial water bodies has facilitated an apparent niche shift; specifically, the expansion into areas of higher evaporation suggests that the presence of more artificial water bodies has shaped the extent of the painted reed frog's novel range. Reports of painted reed frog breeding populations at high-elevation inland locations in South Africa (Bishop, 2004) and a recent colonisation of the dry Western Cape hinterland at Barrydale (see Figure 1; Leslie R. Minter, personal communication) indicate that once these frogs are introduced, they are able to persist in anthropogenic habitats in seemingly unsuitable areas through source-sink dynamics (Davies et al., 2013). If this trend is replicated in the rest of South Africa, the increase in the artificial water bodies that can be used as

stepping stones (Florance et al., 2011) as well as permanent breeding habitats may result in a country-wide range expansion of this species in the future. Together, these results imply an active invasion by painted reed frogs based on the availability of suitable habitats that facilitate range expansion.

Painted reed frogs may have the capacity to further expand their range in South Africa through adaptive mechanisms. Davies et al. (2015) demonstrated plasticity of thermal tolerance and metabolism in the novel range. A broader range of environmental conditions across the novel distribution than the historical one suggests that the species is exposed to conditions which could drive a greater tolerance for dry, hot summer conditions. Such a change in physiological tolerance would allow a shift in the fundamental niche, as found in a few invasive plants (Broennimann et al., 2007) and ectothermic animals (Hill et al., 2013; McCann et al., 2014), and hypothesised for temperate organisms (Pauchard et al., 2016). Although painted reed frogs are highly desiccation resistant, they can lose substantial amounts of body water while active and showed little plasticity of evaporative water loss (Davies et al., 2015). Therefore, if the expansion into drier and more thermally variable areas is accompanied by a change in habitat use or behaviour this could provide additional sheltered microsites around rivers and water bodies to survive dry periods or thermal extremes.

In a study of climatic niche shifts in non-native reptiles and amphibians at a global scale, Li, Liu, Li, Petitpierre, and Guisan (2014) found that the proportion of niche shifts in these taxa was higher than for non-native Eurasian, North American and Australian plants (Petitpierre et al., 2012) or European birds (Strubbe, Broennimann, Chiron, & Matthysen, 2013). Li et al. (2014) found niche expansion metrics of over 10% in only 57% of the amphibian and reptile species studied, although two species showed over 90% niche expansion. Niche unfilling was found for over 80% of the ranges studied, leading Li et al. (2014) to suggest that the niche dynamics they observed may be due to dispersal limitations or altered biotic interactions in the invaded range. One of the most invasive amphibians, the cane toad, showed 13% niche expansion in its invaded Australian range relative to its native range (Tingley et al., 2014). Although it is difficult to directly compare niche metrics between disparate taxa and studies, the level of niche expansion that has accompanied the invasion of painted reed frogs within South Africa is relatively high compared with other studies on herpetofauna and niche overlap is relatively low.

5 | CONCLUSIONS

Our analyses identify a realised niche shift that has allowed painted reed frogs to occupy drier and more thermally variable habitats in their novel (invaded) range. The shift is likely mediated by artificial water bodies that provide additional buffered habitats, a key resource supplement for these small-bodied tropical frogs. The association of water bodies and range expansion in this study provides an important hypothesis of niche change causation in the

painted reed frog. Given that similar patterns of range expansion in response to environmental change have been observed in other species and taxonomic groups (Hickling et al., 2005; Letnic et al., 2014; Okes et al., 2008; Tingley et al., 2014), we suggest that future work on invasive anuran species should consider the niche in terms of both climatic and landscape modification such as artificial water bodies. This would allow more accurate prediction of species invasions and range expansions in future, and help aid conservation strategies. While reciprocal modelling and ordination methods are able to detect signatures of niche shift, experimental evidence is needed to confirm the drivers and mechanisms behind these.

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CONFLICT OF INTEREST

The authors declare no conflict of interest relevant to this work.

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BIOSKETCH

Sarah Davies is interested in the ecology and physiology of range-expanding amphibians in southern Africa and worldwide, and how people can prevent and manage them effectively. This work formed part of her PhD thesis.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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