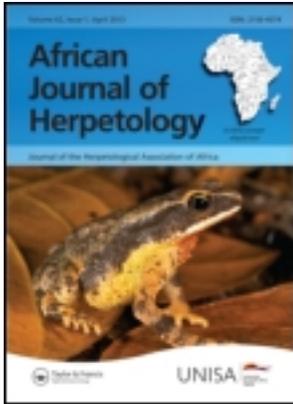


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African Journal of Herpetology

Publication details, including instructions for authors and
subscription information:

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Published online: 22 May 2013.

To cite this article: Clemens Schreiner, Dennis Rödder & G. John Measey (2013): Using modern
models to test Poynton's predictions, African Journal of Herpetology, 62:1, 49-62

To link to this article: <http://dx.doi.org/10.1080/21564574.2013.794865>

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Using modern models to test Poynton's predictions

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Abstract.—In his seminal work ‘The Amphibia of southern Africa: a faunal study’, Poynton identified and contrasted two centres of amphibian importance, the temperate south-western Cape (“Cape”) and tropical northeast (“Tropical”). With reference to the dominant role of climate fluctuations resulting from Milankovitch forcing since the Pliocene, Poynton hypothesised: “These climatic fluctuations must have altered the faunal patterning very considerably, and they have probably left an impression on present distribution”. In this study we use modern methods of species distribution and palaeoclimatic models not available in the 1960s to further investigate Poynton’s predictions on the importance of glacial–interglacial climatic changes on the distributions of southern Africa’s amphibian assemblages. We constructed current distribution models based on presence data for 20 representative endemic anuran taxa from the two centres. We then used two paleoclimatic models (Model for Interdisciplinary Research on Climate: MIROC and Community Climate System Model: CCSM) to project the species’ current niches back to 6 and 21 Kya (Last Glacial Maximum: LGM) to reconstruct hypothetical historical distributions. Our results predict that 65% or 75% of species experienced a range reduction since the LGM, using MIROC and CCSM respectively, but this shrinking was significantly greater in the Cape (mean reduction since LGM = 18 099.6 ± 5 894.27 km² MIROC) than Tropical areas, most of which expanded (mean = - 5 990.3 ± 8 801.80 km² MIROC; $F_{1,18} = 5.074$; $P = 0.037$. CCSM; $F_{1,18} = 15.65$; $P = 0.001$.). Our results are discussed with reference to Poynton’s predictions.

Key words.—Species distribution models, paleoclimate, climatic change, southern Africa, Anura

INTRODUCTION

Recurrent glacial and interglacial shifts, triggered as a response to the collective effect of Milankovitch forces occurred throughout the Quaternary. Milankovitch cycles describe changes in the earth’s orbit around the sun with cycle periods of 10 to 100 Kya (see Bradley 1999; Wilson *et al.* 2000; McDermott *et al.* 2001) and induce insolation changes, which lead to climatic change. Particularly large changes in climatic conditions have occurred during the Pleistocene (Wang *et al.* 1999; Hewitt 2000; Šlechtová *et al.* 2004) with its largest glaciation, at the Last Glacial Maximum (LGM) 18 – 21 Kya, and with a centred temperature optimum in the Holocene 7–4 Kya (Scott & Thackeray 1987; Thackeray 1990). Glaciations led to a spreading of the ice cap that provoked compressions of biomes toward the equator. Due to the great

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Online Supplementary Material is available for this article which can be accessed via the online version of this journal available at www.tandf.co.uk/journals/THER.

amount of water captured by glaciers, seawater volume was reduced causing the emergence of land bridges in several areas of the world (Rohling *et al.* 1998).

Although the LGM was a global event, its expression differed regionally, and the southern African subcontinent is especially complex being influenced by the interface of tropical, subtropical and temperate climate systems and the Indian, Atlantic and southern oceans (Chase & Meadows 2007; see also Tyson 1986; Cockcroft *et al.* 1987, for a general overview of climatic fluctuations during late Quaternary across the subcontinent). Temperate frontal systems embedded in westerlies (Tyson & Preston-Whyte 2000) influence the Winter Rainfall Zone (WRZ) in the southern African Cape, along the western and southern coast. The Summer Rainfall Zone (SRZ) in the north and east is driven by a seasonal interplay between subtropical high-pressure cells and the migration of easterly flow systems interrelated with the Intertropical Convergence Zone (Chase & Meadows 2007). Both zones are thought to respond to global cycles of glacial and interglacial periods in a coeval inverse manner. Glacial periods intensify the WRZ system so that it expands (Cockcroft *et al.* 1987), whereas interglacials intensify the SRZ system, leading to an expanded and more humid SRZ (Cockcroft *et al.* 1987; Tyson 1999). Analyses of speleothems (see Bradley 2006) propose that the mean temperature during the LGM in the southern Africa subcontinent was generally 5.3 to 6° C lower than at present (Heaton *et al.* 1983; Talma & Vogel 1992; Stute & Talma 1997; Kulongoski & Hilton 2004). Furthermore the annual precipitation reached only 40 to 70% of today's level (Partridge *et al.* 1997). Noble gas isotope ratios (Stute & Talma 1997) and pollen records (Scott & Thackeray 1987; Thackeray 1990) show that post-glacial warming began 18 to 17 Kya and reached typical interglacial temperatures 11 to 10 Kya. The warmest times in southern Africa in the Holocene are dated between 7 to 4.5 Kya (Scott & Thackeray 1987; Thackeray 1990) with temperatures as much as 3° above present day conditions (Heaton *et al.* 1983; Partridge 1997; Partridge *et al.* 1999). The dramatic climatic fluctuations which happened during the Pleistocene and Holocene, influenced the environment and likely impacted on the distribution of many taxa, including the amphibians.

The herpetologist John Poynton described just such a context in his seminal work 'The amphibia of southern Africa: a faunal study' (1964a). In this study, he divided the southern African amphibian fauna into biogeographic centres with two main groups which he called "Tropical" and "Cape", terms which we have adopted here. The Tropical fauna has a wide distribution in the north-eastern parts of southern Africa and is species-rich. The Cape fauna is found in the temperate south-west with a restricted distribution and a high concentration of endemics. Closer inspection of the faunal centres reveals that both can be subdivided into highland and lowland centres. Poynton (1964a: 230) hypothesised that for this complex species distribution; "climatic fluctuations must have altered the faunal patterning very considerably, and they have probably left an impression on present distribution". He further hypothesised that during glacial periods the extent of the Cape fauna distribution increased while the extent of distribution of Tropical fauna decreased and *vice versa* for interglacial periods. The two biogeographic centres acted as refuges for species because climate conditions were more stable over time than the surrounding fluctuating habitats. Poynton (1964a) called the subtraction margins where the two faunas overlap the "transitional fauna", which is distributed over large parts of eastern, western and central regions of southern Africa. He assumed, if the area of

climate conditions decreased, it would probably leave isolated disjunct populations in the transitional areas where local conditions are suitable (see also Alexander *et al.* 2004). Parts of Poynton's conclusions (1964a) have since been expanded (see Poynton & Broadley 1978; Poynton 1980, 1987, 1992, 1994, 1999, 2013; Drinkrow & Cherry 1995; Seymour *et al.* 2001, Alexander *et al.* 2004), but an exhaustive evaluation of these theories using modern species distribution models and paleoclimate predictions has never been made.

For these putative refuge-serving areas (see Keppel *et al.* 2012), such as the Tropical and Cape centres described by Poynton (1964a), it is important to gain knowledge about the impacts of climate fluctuations on distribution patterns and to develop appropriate conservation plans, which consider influences of past climatic fluctuations on distribution patterns. Beside climatic fluctuations influenced by Milankovitch cycles, anthropogenic induced climate change impacts the distribution and abundance of amphibian species. Worldwide declines of amphibian populations (Wake 1991; Blaustein & Kiesecker 2002) suggest "that we are in an extinction crisis" (Hilton-Taylor & Mittermeier 2000). Some examples of the serious effects for amphibians of global warming may include raised transmission rates of infectious diseases (Dobson & Carper 1993), changes in phenology (Beebe 1995) and increased global mean temperatures (Nicholls *et al.* 1996) that could accelerate faunal change. In southern Africa, Midgley *et al.* (2001) expected a general increase in temperature with a decrease of summer rainfall between 25% in the south and 5% in the north. Furthermore they suggested a consequential habitat loss between 35–55% of the Fynbos, Succulent Karoo, Grassland and Forest biomes, which would result in a massive loss of breeding habitats and a contraction in range for many species.

To test Poynton's (1964a) hypothesis, we computed species distribution models (SDMs) based on presence data for 20 representative anuran taxa from the lowland and highland Cape and Tropical regions of southern Africa. We used two paleoclimate scenarios for the LGM at 21 Kya and the climatic optimum at 6 Kya to get more detailed insights into Poynton's (1964a) hypothesised impact of climate fluctuation on distribution patterns.

MATERIAL AND METHODS

Study Species

We selected amphibian taxa from the Cape based on their distribution being endemic to the fynbos biome (Fig. 1) to provide a representative mixture of species distributed in montane and lowland habitats. Similarly for Tropical taxa, we selected species only endemic to South Africa's northeast with a mix of montane and lowland forms (Fig. 2). As species had to be endemic, our selection was limited and included a number of species which were not in Poynton's (1964) Tropical assemblage, but his "Transitional" group. We assume that through the shared southern area of their distribution, they are likely to best represent the Tropical group from taxa available to us. Distribution data on the selected taxa were taken from the South African Frog Atlas (Minter *et al.* 2004), using only localities with second accuracy or higher (Table 1). The minimum number of records used for analysis of species was four (*Afrixalus knysnae*) and the maximum number was 81 (*Vandijkophrynus angusticeps*; Table 1).

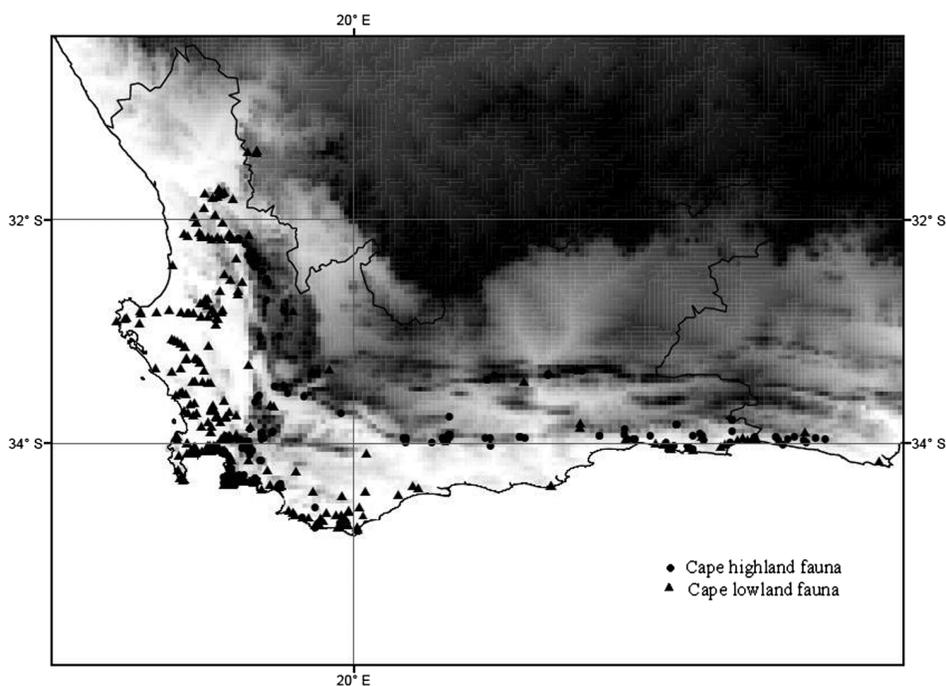


Figure 1. Records of Cape lowland (triangles) and highland (dots) species endemic to fynbos biome.

Climate Data

We used information about current climate from WorldClim 1.4 (Hijmans *et al.* 2005) based on weather data from 1950 to 2000 with a grid cell resolution of 30 arc sec. We obtained information on the paleoclimate of the LGM 21 Kya and the Mid-Holocene 6 Kya derived from the Community Climate System Model (CCSM; Hijmans *et al.* 2005; www.cesm.ucar.edu) and the Model for Interdisciplinary Research on Climate 3.2 (MIROC; www.ccsr.u-tokyo.ac.jp/~hasumi/MIROC/). Palaeoclimates were downscaled to a spatial resolution of 2.5 arc minutes following the delta method described in Peterson and Nyári (2007). A correlation matrix based on squared Pearson's correlation coefficients computed to select eleven bioclimatic factors with low co-linearity ($R^2 < 0.75$) for further analysis. Bioclimatic factors included annual mean temperature, mean diurnal range (max. temp- min. temp-) (monthly average), isothermality, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation seasonality (coefficient of variation), precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter (Supplementary Information 1).

Species Distribution Modelling

We used a machine-learning algorithm following a maximum entropy approach to compute the species' potential distributions based on environmental predictors (i.e.,

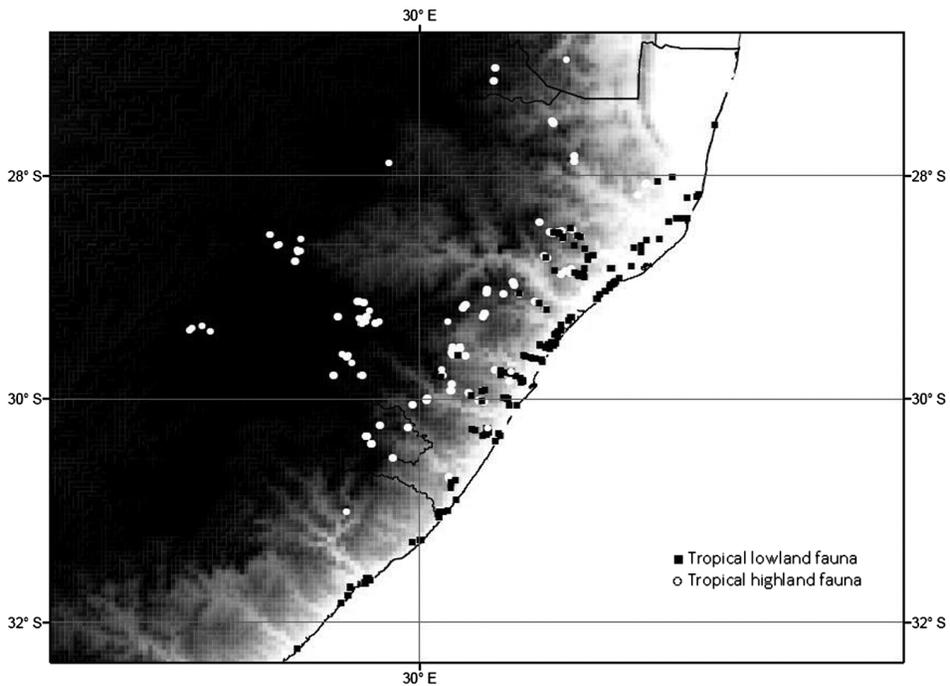


Figure 2. Records of Tropical lowland (black squares) and highland (white dots) species endemic to South Africa's northeast.

MaxEnt 3.3.3k; Phillips *et al.* 2006). We repetitively computed 100 unique random data sets allocating 70% of the available records per species to training data and 30% to test data, which were used for model validation via the Area under Curve (AUC) of the Receiver Operating Characteristic Curve (ROC) (Pearce & Ferrier 2000). AUC, as parameter for evaluating the predictive ability of the model (Scheldeman & van Zonneveld 2010), was used as a quality measure of the discrimination ability of the SDM. Values of AUC range from 0.5, for models with random predictions to 1.0, for models giving perfect predictions. As environmental background, we selected those grid cells within a circular buffer of 100 km enclosing the respective species records. The average projections across all 100 replicates per species onto current and paleoclimate conditions were transformed into binary maps applying the average minimum training presence and average 10% training omission thresholds. Occurrence of non-analogous climatic conditions requiring *a priori* extrapolation of the SDM were quantified via Multivariate Environmental Similarity Surfaces (MESS) following Elith *et al.* (2011). Projections into non-analogous climates may increase the potential for extrapolation and interpolation errors (Elith *et al.* 2011, Engler & Rödder 2012). Potential areas of occurrence were computed based on presence-absence maps applying the minimum training presence threshold using the respective functions in the raster package for R (i.e., 'area') but excluding extrapolation areas as identified by MESS. Further analyses (paired t-tests and ANOVA) were conducted in R (R Core Team 2012). Means are given \pm Standard Error.

Table 1. Number of records, ecological properties and predicted range of distributions (km²) for 20 southern African anuran taxa. Species are sorted after Poynton's (1964a) Cape (C) and Tropical (T) fauna and are furthermore divided into lowland (L) and highland (H) species for each division. Last column indicates the agreement of models to Poynton's predictions for 21K models, 6K models, both (yes) and neither (no) (+ = agreement only in CCSM; * = agreement only in MIROC)

Species	Records	Ecological properties		Predicted range of frog distributions (km ²)					Agreement to Poynton
		Area	Altitude	Current	CCSM 6k	CCSM 21k	MIROC 6k	MIROC 21k	
<i>Arthroleptis wahlbergi</i>	70	T	H	287247	272465.3	277161.6	270290	281515.9	21k
<i>Afrivalus knysnae</i>	4	C	L	3640.4	2801.9	1744.7	2698	181.2	6k
<i>Amietia vandijki</i>	12	C	H	6397.4	10152.0	13005.5	12338.9	54035.7	21k
<i>Arthroleptella villiersi</i>	17	C	H	4142.1	5669.1	16485.9	5683.3	14969.3	21k
<i>Breviceps bagginsi</i>	7	T	L	236857.8	228303.1	237413.8	227926.8	237211.5	no
<i>Breviceps acutirostris</i>	10	C	H	15185.3	19445.1	20024.2	22048.1	58855.2	21k
<i>Breviceps fuscus</i>	16	C	H	22171.0	22917.7	17574.1	25926.4	36113.6	21k*
<i>Breviceps gibbosus</i>	18	C	L	7567.7	7494.7	3465.1	8159.6	3860.7	6k*
<i>Cacosternum capense</i>	21	C	L	14733.1	11154.4	1352.4	9185.8	787.6	6k
<i>Hadromophryne natalensis</i>	31	T	H	545702.8	545987.4	516289.8	515188.8	524684.3	21k & 6k +
<i>Heleophryne purcelli</i>	27	C	H	21909.5	23870.0	51956.2	29716.5	74720.9	21k
<i>Heleophryne regis</i>	8	C	H	7787.4	8772.4	1235.5	8967.8	7494.4	No
<i>Hyperolius horstockii</i>	27	C	L	25518.7	23533.2	32375.7	23060.1	65132.2	Yes
<i>Leptopelis xenodactylus</i>	7	T	H	211184.5	205159	185244.9	187386.9	215606.4	21k +
<i>Leptopelis natalensis</i>	68	T	L	247561.5	243089.2	227965.2	240726.1	209371.7	21k
<i>Microbatrachella capensis</i>	7	C	L	5276.5	5561.0	18359.0	5506.8	14331.5	21k
<i>Poyntonia paludicola</i>	12	C	H	4622.6	4871.7	15203.3	5013.6	14583	21k
<i>Strongylopus wageri</i>	7	T	H	379619.4	349556.2	304828	335767.1	403841.2	21k +
<i>Vandijkophrynus angusticeps</i>	81	C	L	80269.7	81509.1	93764.5	81631.2	120400.6	21k
<i>Xenopus gilli</i>	9	C	L	3925.4	3961.1	13524.9	3960.8	11074.6	21k

RESULTS

We received, on average ($n = 100$) training AUC-Values of 0.937 and test AUC-Values of 0.904 in the models for all tested species (Supplementary Information 2). The analyses of the contribution of bioclimatic factors to the model show that the 'precipitation of warmest quarter' and the 'mean temperature of warmest quarter' had the highest explanative power for Tropical fauna whereas the 'precipitation of coldest quarter' and the 'mean diurnal range' had the highest explanative power for Cape fauna (Supplementary Information 1). The mean of all average minimum training presence thresholds was 0.25 ± 0.138 and the mean of all average lowest 10 percentile training omission thresholds was 0.346 ± 0.071 (Supplementary Information 2).

On average, the differences for the predicted range in comparison to the current range for our sample of frog distributions at 21 Kya (CCSM 102 448.7 \pm 31 767.57 km²; MIROC 117 438.6 \pm 33 294.31 km²) was similar to the current modelled range (106 566.0 \pm 35 095.43 SD km²) and that modelled for 6 Kya (CCSM 103 813.7 \pm 34 083.10 km²; MIROC 101 059.1 \pm 32 513.21 km²), and no mean changes with respect to current predicted distributions were significant. However, when the areas in which the frogs occurred (Cape and Tropical) were taken into account, the Cape fauna was predicted to have much larger ranges for projections at 21 Kya (CCSM 21 433 \pm 6 641 km²; Paired-t = -2.497; P = 0.084; MIROC 34 038.6 \pm 9 557.64 km²; Paired-t = 3.071; P = 0.009) than present (15 939.3 \pm 9 557.64 km²), but this was not the case for Tropical frogs (current 318 028.8 \pm 51 493.19 km²; CCSM 291 483.9 \pm 48 015.90 km²; Paired-t = -2.497; P = 0.054; MIROC 312 038.5 \pm 51 645.04 km²; Paired-t = -0.681; P = 0.526). No further significant explanatory differences could be found when frog distributions were further subdivided into highland and lowland species.

Among six tested Tropical species five models for 21 Kya and one for 6 Kya showed consistency with Poynton's predictions. For those species from the Cape, nine models for 21 Kya and three for 6 Kya of the 14 Cape species agreed with Poynton's predictions. For both, 6 Kya and 21 Kya, one species fulfilled Poynton's predictions.

Tropical Highland Fauna

Arthroleptis wahlbergi showed a reduced potential distribution from present to 6 Kya and 21 Kya. The potential distribution for *Leptopelis xenodactylus* and *Strongylopus wageri* became reduced in 6 Kya models, but paleoclimatic models for both of these species at 21 Kya revealed greater and reduced potential distribution, respectively. In contrast, the potential distribution for *Hadromophryne natalensis* revealed greater and reduced potential distribution in 6 Kya models, but paleoclimatic models for these species showed decreased potential distributions at 21 Kya.

Tropical Lowland Fauna

Breviceps bagginsi, mainly distributed in the eastern parts of Maputaland-Pondoland, showed a reduced potential distribution 6 Kya, but for 21 Kya they revealed for this species greater potential distributions. The paleoclimatic models for *Leptopelis*

natalensis (Fig. 3) showed a reduced potential distribution from present to 6 Kya and 21 Kya. Both models exhibited a considerable contraction of the climate determined range into the north east at 21 Kya for *Leptopelis natalensis* (Fig. 3).

Cape Lowland Fauna

All investigated species, principally distributed in the lowlands in the south-western parts of southern Africa, live in narrow ranges of suitable climate conditions. The potential distribution for *Hyperolius horstockii*, *Microbatrachella capensis* (Fig. 4), *Vandijkophrynus angusticeps* and *Xenopus gilli* changed somewhat 6 Kya and became greater with a shift to the exposed Agulhas shelf area from 6 Kya to 21 Kya. In contrast to the results mentioned above, the potential distribution of *Afrixalus knysnae* and *Cacosternum capense* was reduced from present to 6 Kya and 21 Kya.

Cape Highland Fauna

Those species, which were mainly distributed in the south-western highlands of southern Africa, also live in small areas of suitable climate conditions. The potential distributions of *Poyntonia paludicola*, *Amietia vandijki*, *Arthroleptella villiersi* and *Breviceps acutirostris* are greater and shifted to the exposed Agulhas shelf area from present to 6 Kya and 21 Kya. The paleoclimatic models for *Breviceps fuscus* also revealed similar pattern with a greater potential distributions and shift to the exposed Agulhas shelf area with the difference that CCSM showed a reduction in the potential distribution 21 Kya. The paleoclimatic models for *Heleophryne regis* showed a reduced potential distribution 6 Kya, but for 21 Kya they revealed greater potential distributions. The paleoclimatic model CCSM computed no shift of climate conditions for this species on the exposed Agulhas plain 21 Kya.

DISCUSSION

Of the world's terrestrial regions, the southern African Cape has had the most stable climate during the Quaternary, despite Milankovitch climate oscillations (Dynesius & Jansson 2000). This climatic stability is considered to be the major contributing factor in the incredible floral diversity of the Cape Floristic Region (Hopper 2009). It may be that this climatic stability has also promoted amphibian diversity in the region, although evidence for this is currently scant (see Tolley *et al.* 2010). In this study, we found that our models predicted that the distribution of frogs in the Cape at the LGM were likely to be approximately three times their current range, while the size of the distribution of Tropical frogs was around the same. In this respect, our findings agree with Poynton's (1964a) hypothesised patterns of increased amphibian distributions in the Cape. However, a northern expansion of Cape species is not predicted by our models (*sensu* Alexander *et al.* 2004; Fig. 1), instead much of the range expansions are predicted to be southwards onto the exposed Agulhas bank. Thus, the current distribution of Cape frogs likely reflects a refuge area for many of these species.

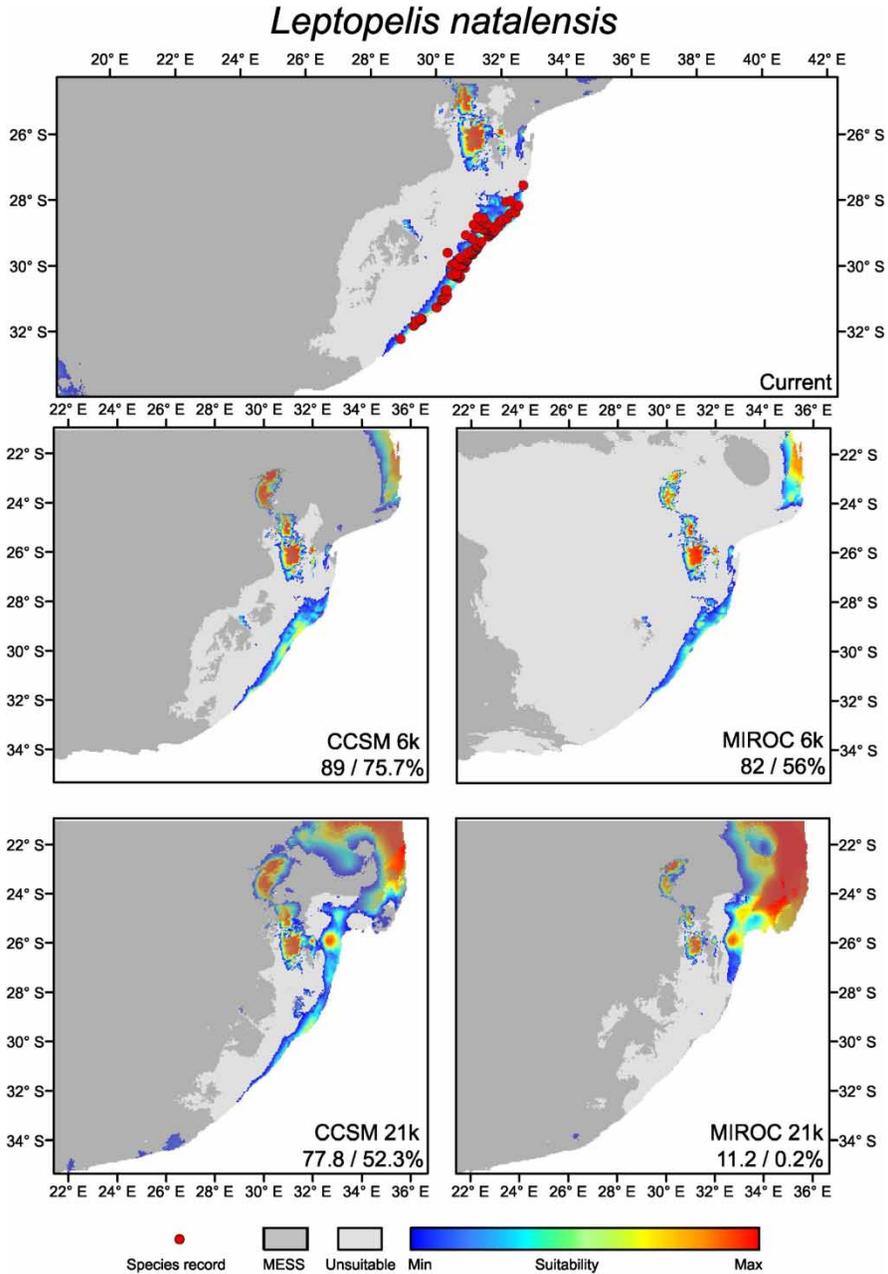


Figure 3. Present distribution of *Leptopelis natalensis* in southern Africa and potential distribution (CCSM 6 and 21 Kya as well as MIROC 6 and 21 Kya) computed with MaxEnt 3.3.3k affiliate from current climatic conditions. Dots represent species records used for model training. Dark-grey areas represent MESS regions with non-analogue climate. Light-grey areas represent regions with unsuitable climate conditions for the species. First percentage declaration represent minimum training presence threshold while the following shows 10% training omission threshold.

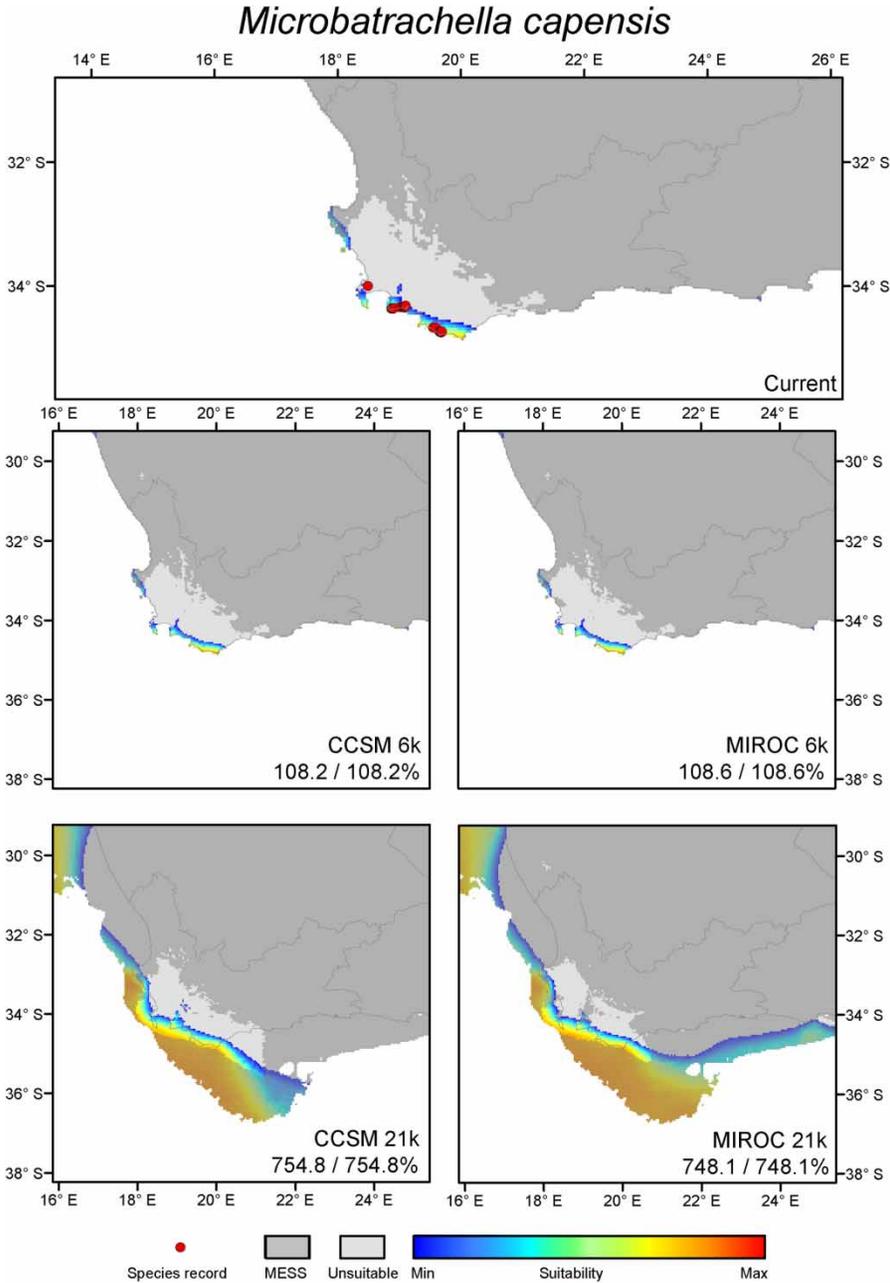


Figure 4. Present distribution of *Microbatrachella capensis* in southern Africa and potential distribution (CCSM 6 and 21 Kya as well as MIROC 6 and 21 Kya) computed with MaxEnt 3.3.3k affiliate from current climatic conditions. Dots represent species record used for model training. Dark-grey areas represent MESS regions with non-analogue climate. Light-grey areas represent regions with unsuitable climate conditions for the species. First percentage declaration represent minimum training presence threshold while the following shows 10% training omission threshold.

Our models suggest that Tropical species, like *Strongylopus wageri*, *Leptopelis natalensis* (Fig. 3) or *Breviceps bagginsi*, may have been distributed further north with a southward range shift since the LGM. These results underpin Poynton's (1964a) suggestions of a stable climate in range restricted Cape fauna serving as refuge, but a more wide ranging Tropical fauna. But there was no universal agreement of Cape and Tropical distribution to Poynton's predictions as a small amount of tested species showed opposite distribution patterns. The potential climate conditions for Tropical species, like *Breviceps bagginsi* and for Cape species, like *Afrivalus knysnae* and *Cacosternum capense*, indicate the opposite of the hypothesised distribution trends, with an increased range in Tropical species and a smaller range of Cape species distribution at the LGM. Projections onto the two paleoclimate scenarios suggest different patterns of potential distributions for some species, e.g., *Leptopelis xenodactylus* and *Strongylopus wageri* since the LGM. For these species it is hard to interpret any potential historical distribution along with climate conditions.

Our results suggest that it is unlikely that glacial fluctuations alone can explain formation of the unique Cape amphibian fauna. Phylogenetic divisions within and between some species pre-date the Quaternary, instead pointing to other events such as the uplifting of the eastern subcontinent during the Miocene (20 Mya; Tolley *et al.* 2010). However, there are some important caveats that must be considered along with the results from our species distribution models. Potential climate conditions are only a proxy for historical species distributions. For species like *Hyperolius horstockii*, with cosmopolitan habitat types (Braack 2004), paleoclimatic scenarios are likely to be more accurate. But for habitat specialists, such as *Xenopus gilli* which lives in acid blackwater wetlands in lowland coastal Fynbos sites (de Villiers 2004) our paleoclimatic scenarios are unlikely to predict the existence of specific habitat types. Similarly, the Tropical amphibian forest fauna are thought to be closely associated with Afrotropical forest paleoreugia (Lawes *et al.* 2007). We also acknowledge that where we had scant distribution data (e.g., *Afrivalus knysnae*), our models are more likely to produce erroneous predictions of distribution. In addition, the models that we used to predict past climate scenarios are far from perfect, and are likely to change significantly in the future as more paleoclimatic data becomes available (see Chase & Meadows 2007), just as they have in the past 60 years since Poynton's monograph (Poynton 1964a).

The precipitation of the warmest quarter and the mean temperature of warmest quarter were the most explanative bioclimatic factors for the Tropical fauna, covered by the Summer Rainfall Zone (SRZ) with a mean annual precipitation of > 66% between April and September (Supplementary Information 1), and this corresponds to the summer breeding period for most of these species. For the Cape fauna, covered by the Winter Rainfall Zone (WRZ) with a mean annual precipitation of > 66% between October and March, the precipitation of the coldest quarter was the most explanative bioclimatic factor (Supplementary Information 1), which similarly corresponds to these winter breeders. Poynton suggested that only temperature exerts a direct correlation with faunal change and shows a contemporary correlation with distribution (Poynton 1964a, b). Precipitation on the other hand acts historically more transitory, indirectly through effects on habitat (Poynton 1964a). Poynton (1964a) did not consider the patterns of amphibian distribution as simple direct reflections of ecological patterns as he considered that amphibians have wide ecological tolerances. Although our models are not predictive in terms of future

climate change, they do suggest that the distribution of amphibians in both areas is sensitive to climate, particularly in the Cape, and that it would be worthwhile continuing to develop better models for conservation planning.

CONCLUSIONS

The paleoclimate scenarios for some Tropical and Cape amphibians are in broad support of Poynton's (1964a) hypothesised patterns of distribution. Since the LGM Cape species are predicted to have experienced a decrease in distribution along with the loss of the shelf area of the Agulhas bank, while some Tropical species could have experienced an increase in distribution range with a shift from the north, southward along with suitable climate conditions. However this correlation was not universally applicable. Some important caveats, like habitat specialisation, must be considered prior to making firm conclusions, and we suggest caution in the interpretation of these potential climate conditions which are serve as hypothetical proxies for historical species distributions.

ACKNOWLEDGEMENTS

This contribution was inspired by the visionary works of John Poynton, to whom we dedicate this work. We acknowledge the great many people that contributed records to the South African Frog Atlas Project and the Animal Demography Unit, University of Cape Town for making those records available. Many thanks to Simon Loader for inviting us to contribute to this special issue.

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Received: 7 November 2012; Final acceptance: 8 April 2013

SUPPLEMENTARY INFORMATION 1

Contribution of the bioclimatic factors annual mean temperature (BIO 1), mean diurnal range (BIO 2), isothermality (BIO 3), mean temperature of wettest quarter (BIO 8), mean temperature of driest quarter (BIO 9), mean temperature of driest quarter (BIO 10), mean temperature of coldest quarter (BIO 11), mean temperature of coldest quarter (BIO 15), precipitation of driest quarter (BIO 17), precipitation of warmest quarter (BIO 18) and precipitation of warmest quarter (BIO 19) for the models of 20 southern African anuran taxa.

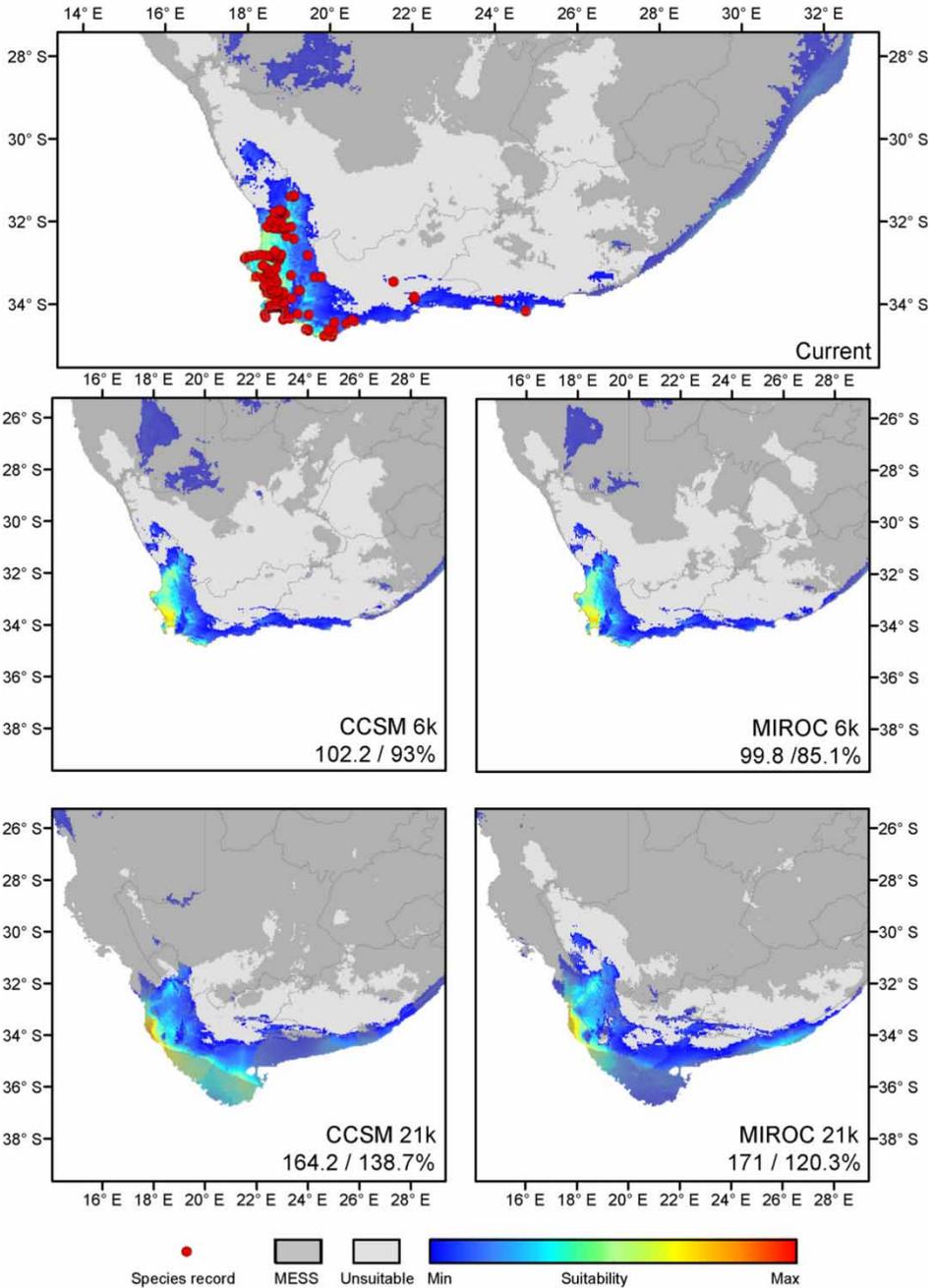
Species	Contribution of bioclimatic factors										
	BIO1	BIO2	BIO3	BIO8	BIO9	BIO10	BIO11	BIO15	BIO17	BIO18	BIO19
<i>Arthroleptis wahlbergi</i>	2.2	11.6	6.0	0.9	0.5	0.6	3.4	7.2	41.4	24.7	1.4
<i>Afrixalus knysnae</i>	1.5	31.3	2.9	0.1	4.9	0.2	14.4	9.1	7.6	10.6	17.4
<i>Amietia vandijki</i>	5.9	0.6	0.5	2.9	4.0	44.5	3.2	22.5	3.3	6.8	5.9
<i>Arthroleptella villiersi</i>	5.5	40.9	15.1	0.0	0.5	2.2	5.7	0.6	1.0	0.3	28.3
<i>Breviceps bagginsi</i>	0.2	3.5	40.1	0.0	0.1	29.2	0.1	1.1	0.5	24.5	0.7
<i>Breviceps acutirostris</i>	5.8	1.0	0.6	0.9	6.7	26.9	3.1	0.4	47.0	2.0	5.6
<i>Breviceps fuscus</i>	0.2	0.9	13.0	0.2	1.8	0.1	1.3	10.0	46.9	22.2	3.5
<i>Breviceps gibbosus</i>	4.0	3.1	3.8	14.6	0.8	2.5	7.6	8.7	2.9	0.4	51.8
<i>Cacosternum capense</i>	0.1	29.8	4.0	41.6	0.3	1.1	0.3	1.4	9.6	7.2	4.6
<i>Hadromophryne natalensis</i>	0.9	1.0	14.8	2.5	2.5	26.4	0.6	0.6	5.4	41.2	4.1
<i>Heleophryne purcelli</i>	31.6	1.2	7.1	0.7	2.2	6.3	9.5	10.9	1.5	0.3	28.7
<i>Heleophryne regis</i>	0.0	0.6	11.9	0.4	1.2	1.2	0.2	25.5	15.7	43.2	0.1
<i>Hyperolius horstockii</i>	0.5	81.7	4.2	0.2	1.6	0.6	1.7	4.3	0.7	0.8	3.7
<i>Leptopelis xenodactylus</i>	0.4	7.5	5.1	0.4	0.6	6.9	0.4	1.6	0.1	76.8	0.1
<i>Leptopelis natalensis</i>	2.8	18.9	6.8	0.2	6.7	3.2	4.6	2.7	1.1	12.5	40.6
<i>Microbatrachella capensis</i>	0.0	88.1	2.7	0.0	0.0	2.9	0.7	2.4	0.0	0.4	2.8
<i>Poyntonia paludicola</i>	2.4	38.8	2.5	0.1	1.7	2.4	0.5	2.2	21.9	2.9	24.7
<i>Strongylopus wageri</i>	0.9	16.0	4.6	2.0	2.6	20.8	0.4	8.5	0.5	38.1	5.7
<i>Vandijkophrynus angusticeps</i>	3.0	6.1	2.1	5.2	2.1	1.5	11.3	25.7	5.7	2.0	35.1
<i>Xenopus gilli</i>	0.0	86.6	0.1	0.1	0.5	0.7	0.9	5.5	0.0	0.1	5.5

SUPPLEMENTARY INFORMATION 2

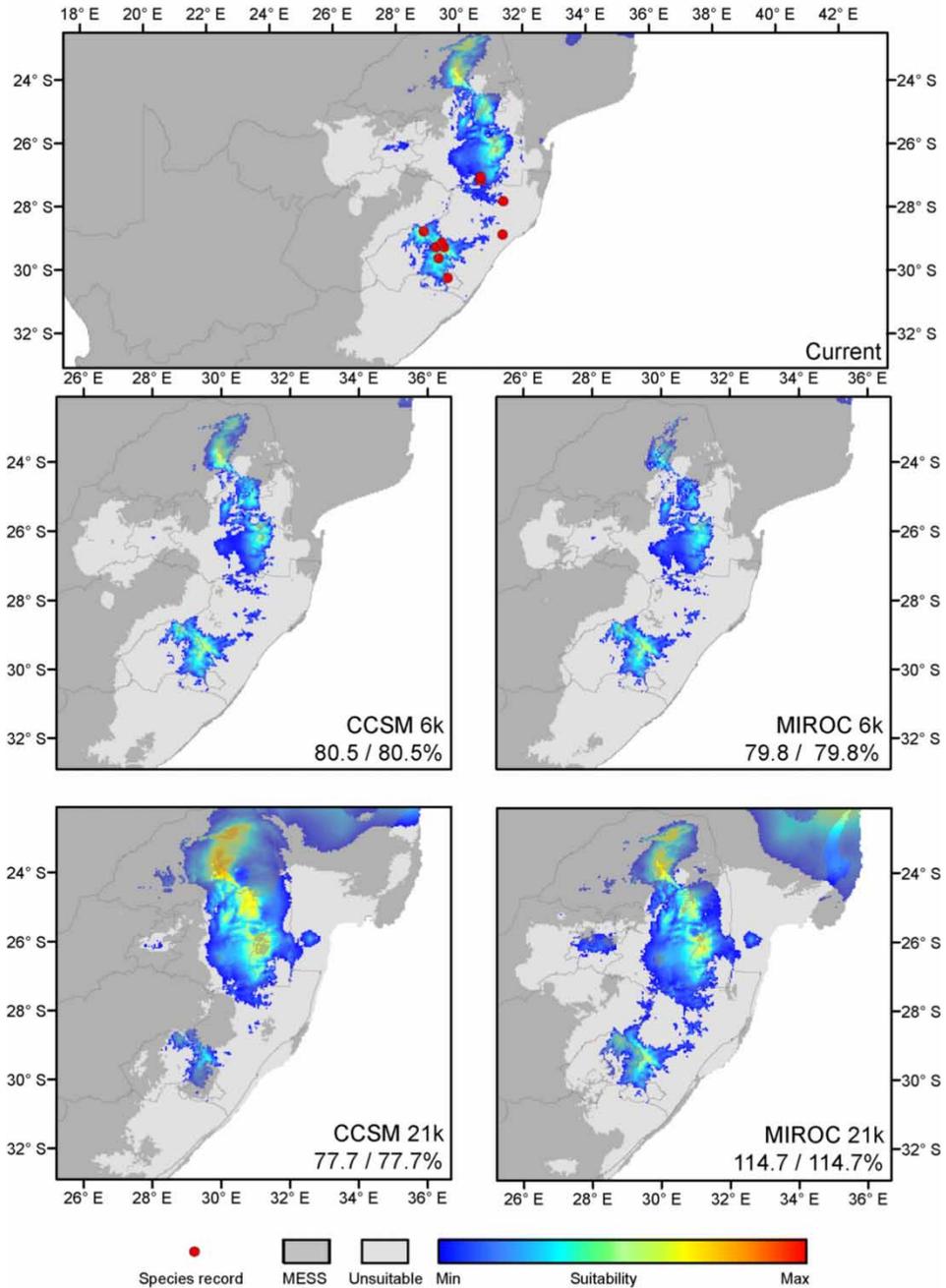
Minimum training presence thresholds (Minimum) and 10% training omission threshold (10%) as well as the model validation via the Area under Curve (AUC) (training and test) for 20 southern African anuran taxa.

Species	Model validation		Thresholds	
	Training AUC	Test AUC	Minimum	10%
<i>Arthroleptis wahlbergi</i>	0.89	0.85	0.0703	0.3328
<i>Afrixalus knysnae</i>	0.96	0.90	0.4758	0.4758
<i>Amietia vandijki</i>	0.97	0.96	0.311	0.4139
<i>Arthroleptella villiersi</i>	0.98	0.96	0.1568	0.2659
<i>Breviceps bagginsi</i>	0.86	0.82	0.4153	0.4153
<i>Breviceps acutirostris</i>	0.94	0.91	0.2865	0.3817
<i>Breviceps fuscus</i>	0.97	0.94	0.0957	0.2182
<i>Breviceps gibbosus</i>	0.96	0.93	0.275	0.3953
<i>Cacosternum capense</i>	0.93	0.89	0.2611	0.4011
<i>Hadromophryne natalensis</i>	0.94	0.91	0.0807	0.2311
<i>Heleophryne purcelli</i>	0.96	0.93	0.0858	0.2798
<i>Heleophryne regis</i>	0.96	0.93	0.3812	0.3812
<i>Hyperolius horstockii</i>	0.96	0.94	0.0865	0.2257
<i>Leptopelis xenodactylus</i>	0.90	0.87	0.3775	0.3775
<i>Leptopelis natalensis</i>	0.94	0.92	0.0957	0.2991
<i>Microbatrachella capensis</i>	0.94	0.93	0.3683	0.3683
<i>Poyntonia paludicola</i>	0.95	0.94	0.3229	0.3901
<i>Strongylopus wageri</i>	0.83	0.71	0.3726	0.3726
<i>Vandijkophrynus angusticeps</i>	0.94	0.90	0.0464	0.3028
<i>Xenopus gilli</i>	0.96	0.95	0.3683	0.3683

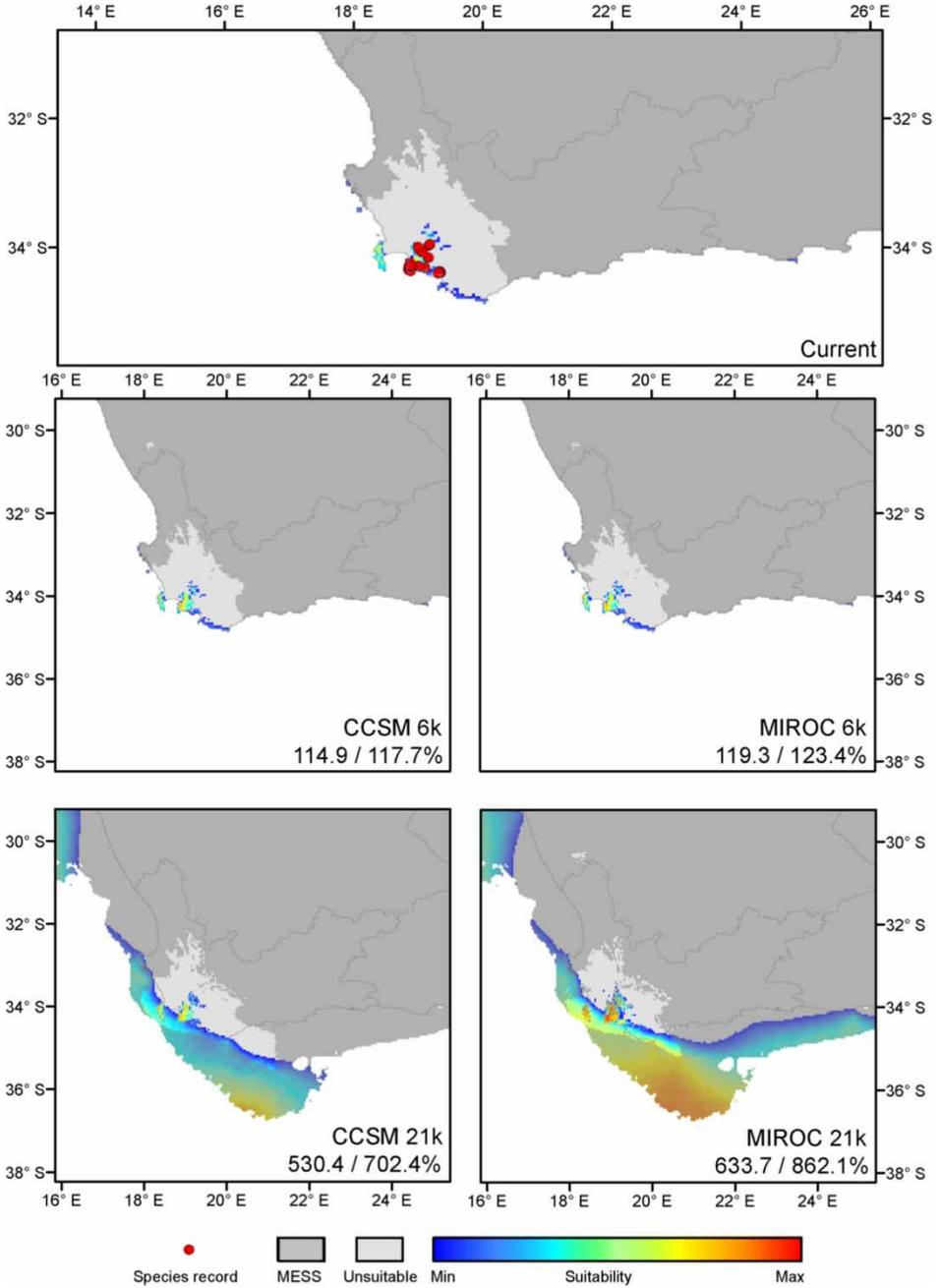
Vandijkophrynus angusticeps



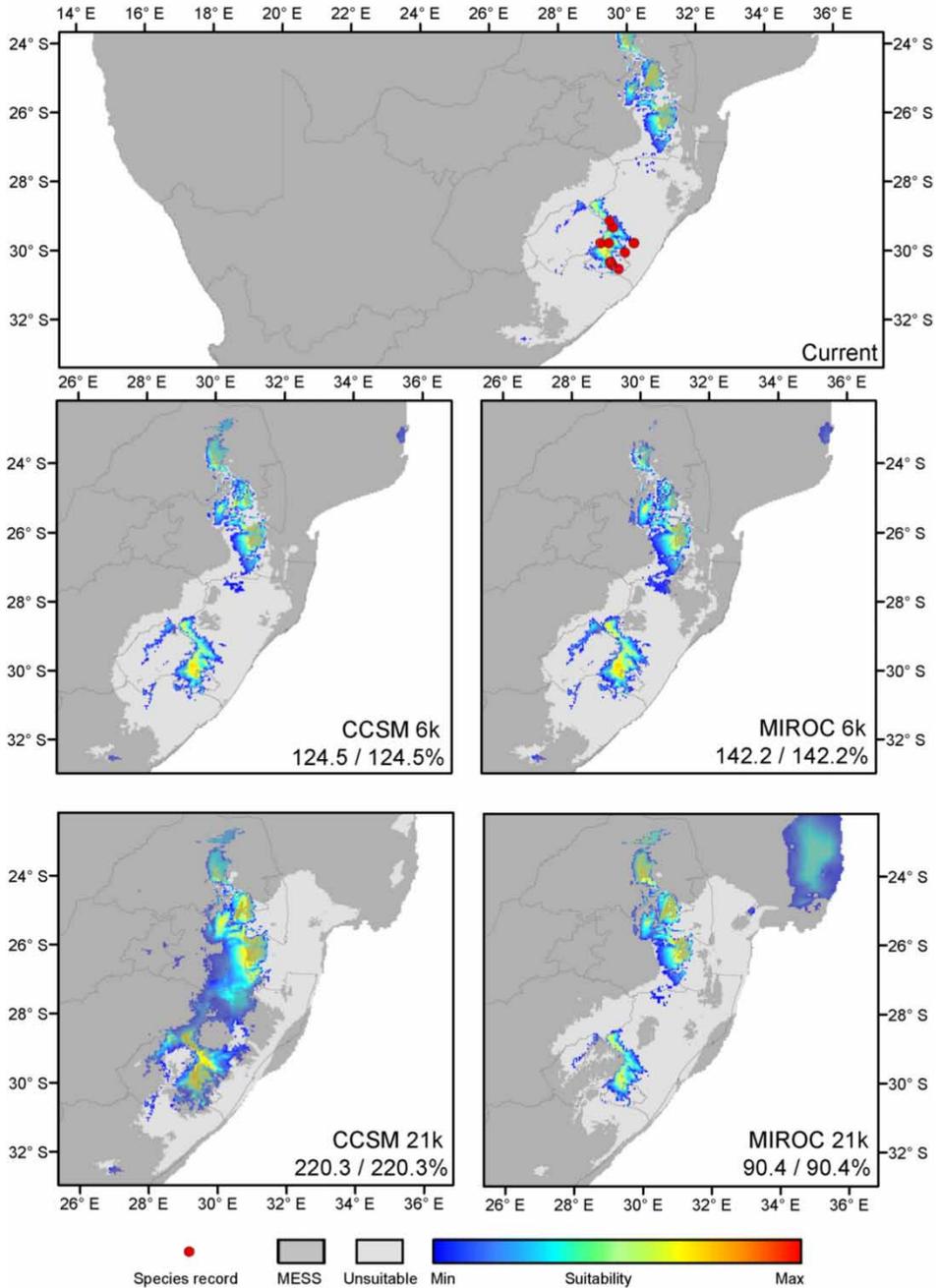
Strongylopus wageri



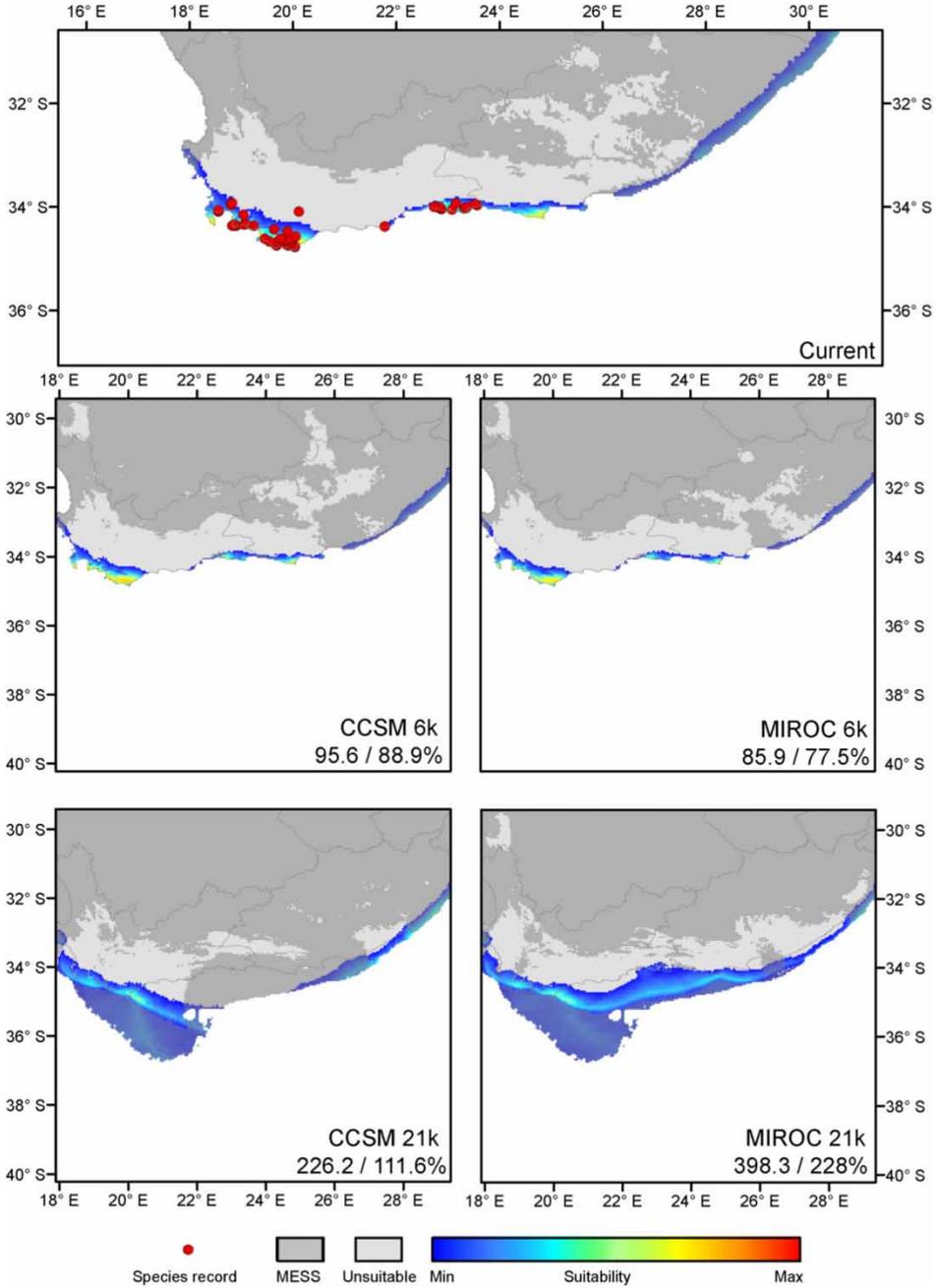
Poyntonia paludicola



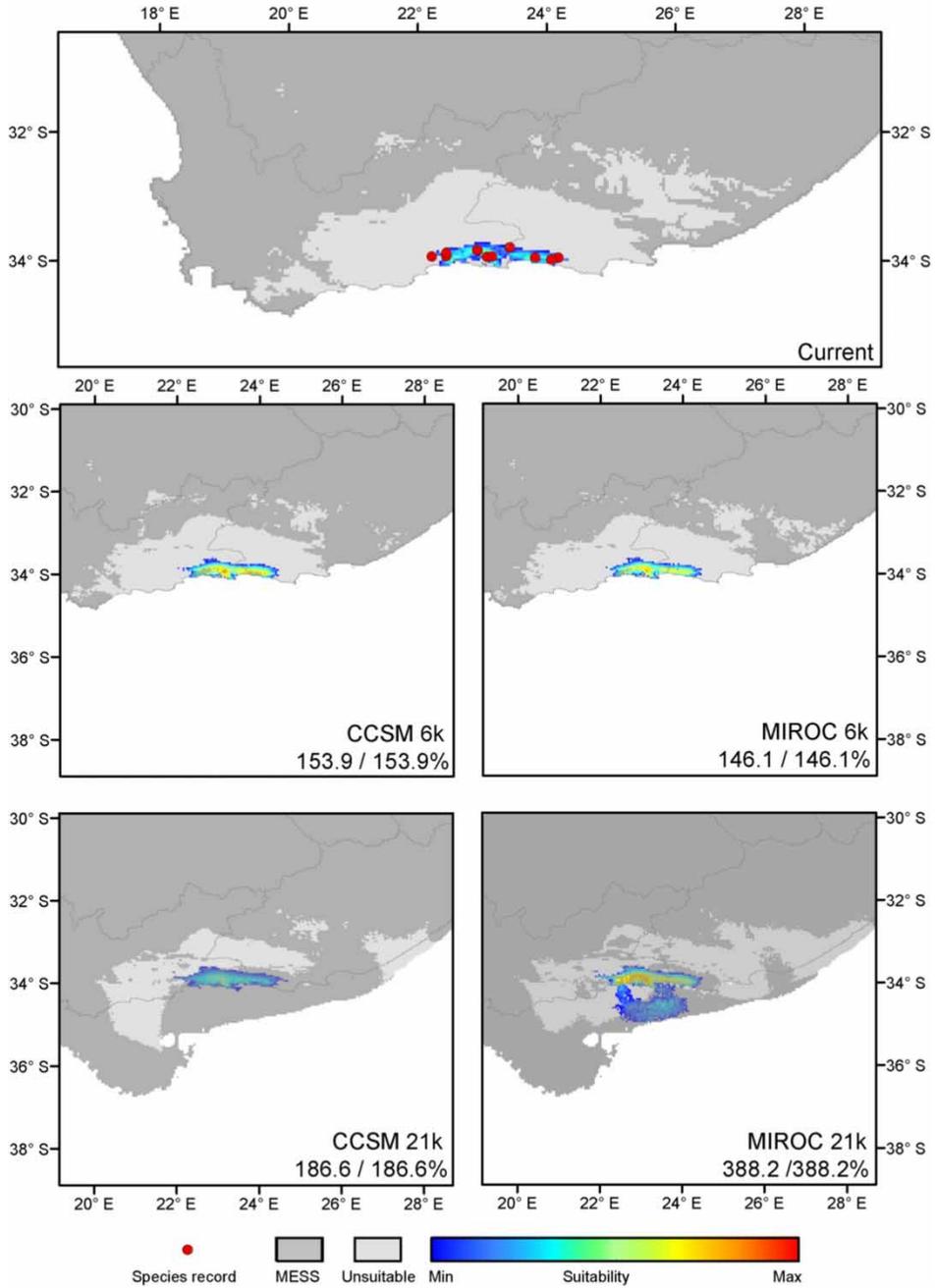
Leptopelis xenodactylus



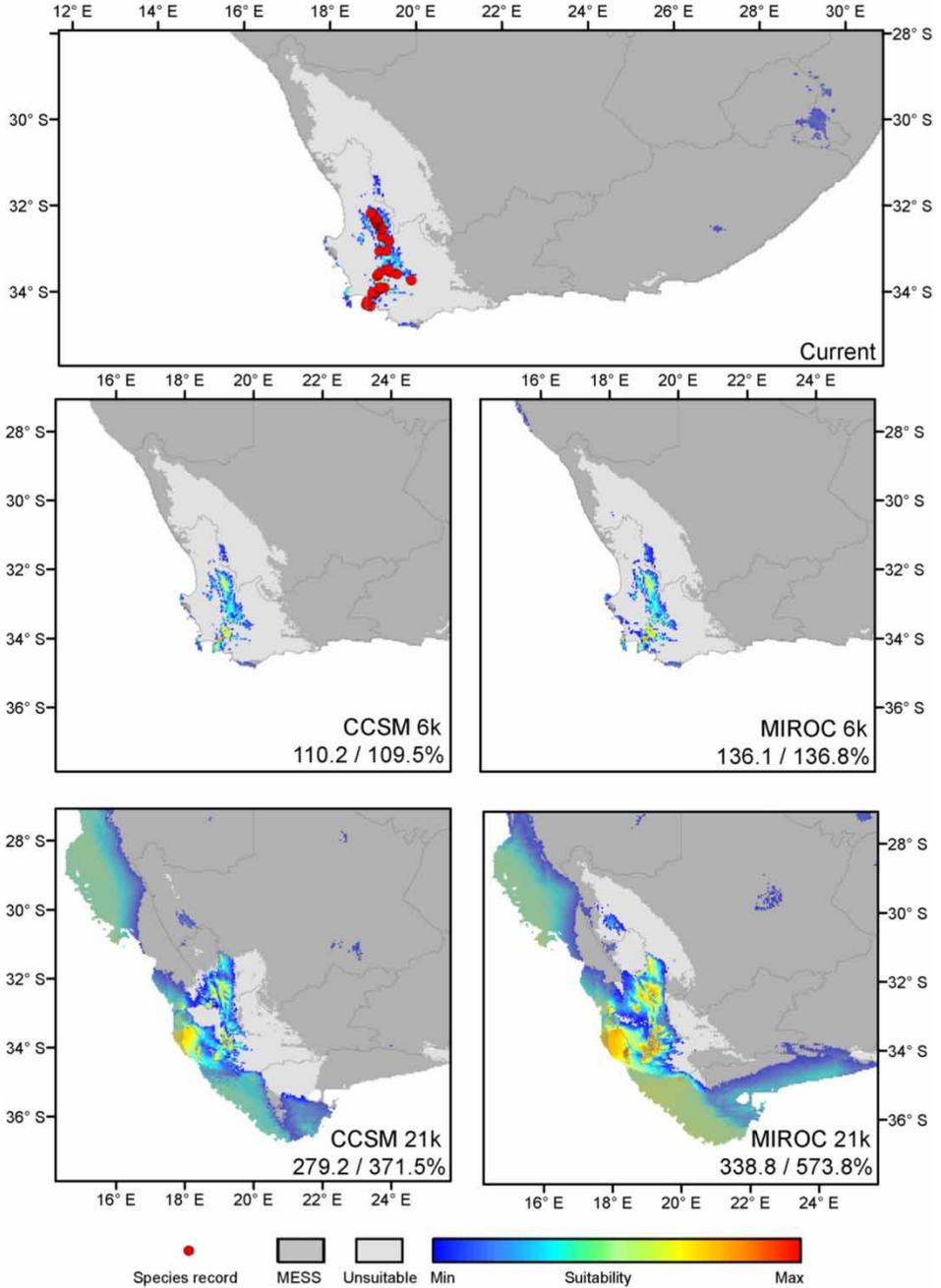
Hyperolius horstockii



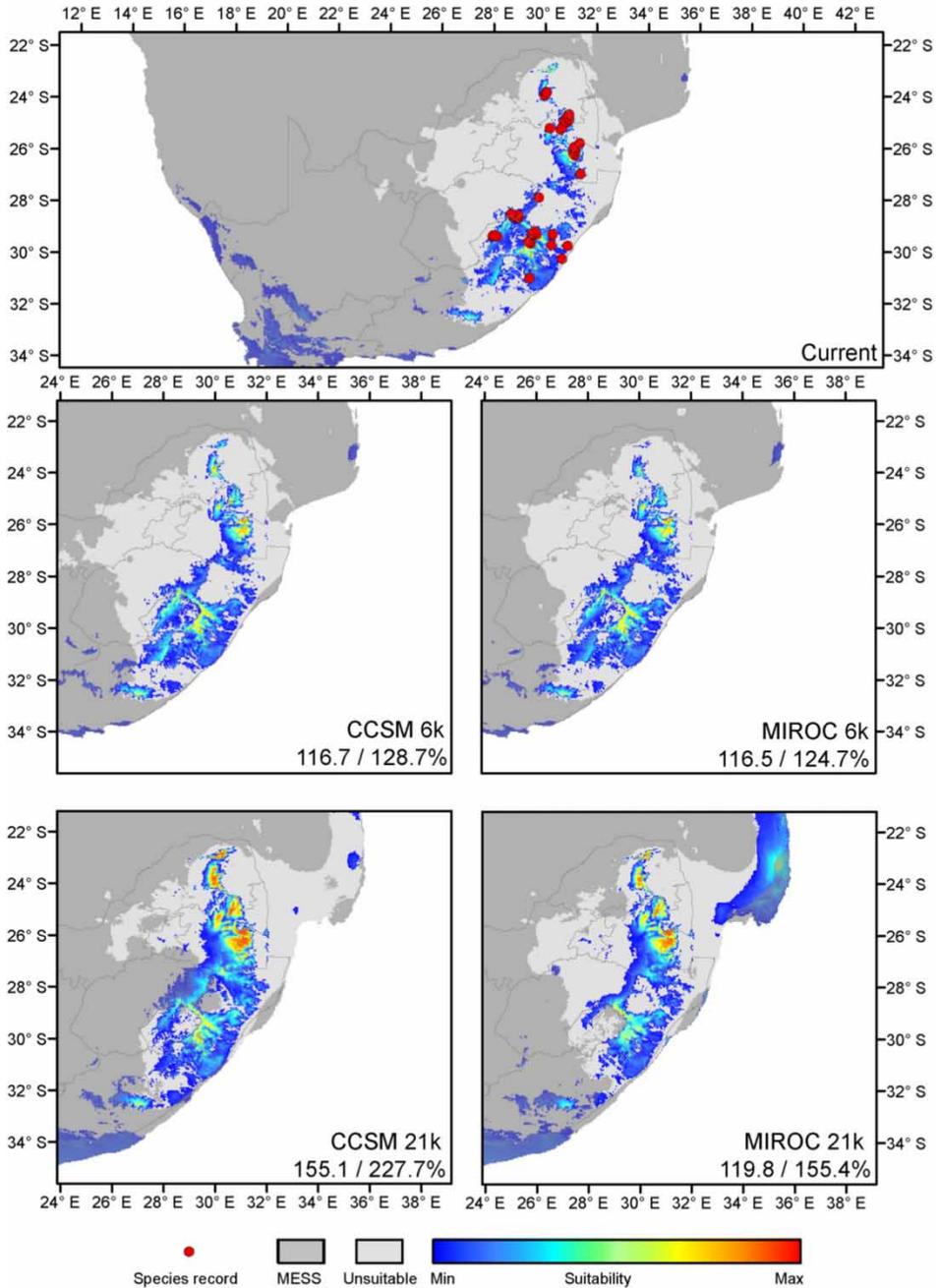
Heleophryne regis



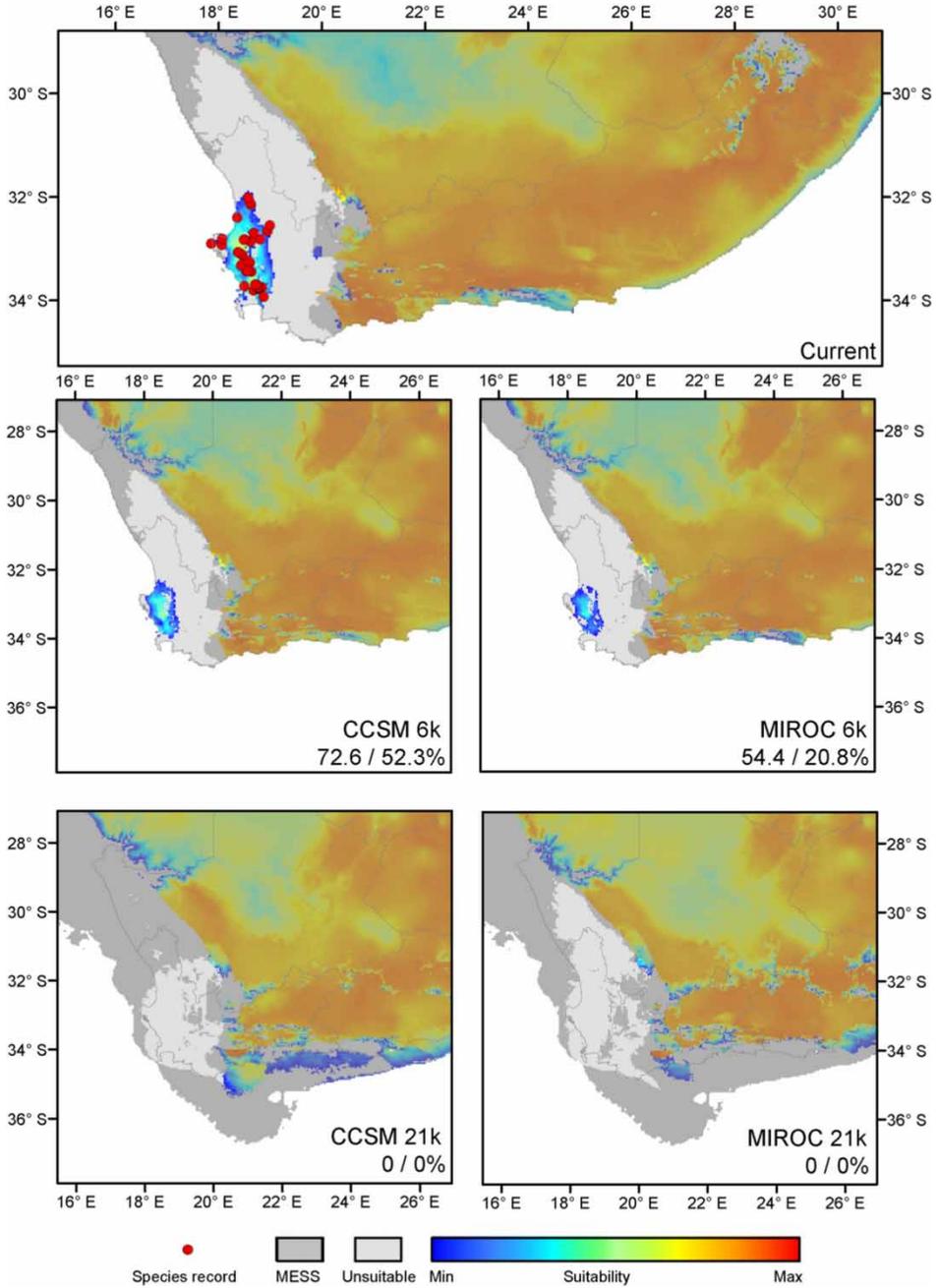
Heleophryne purcelli



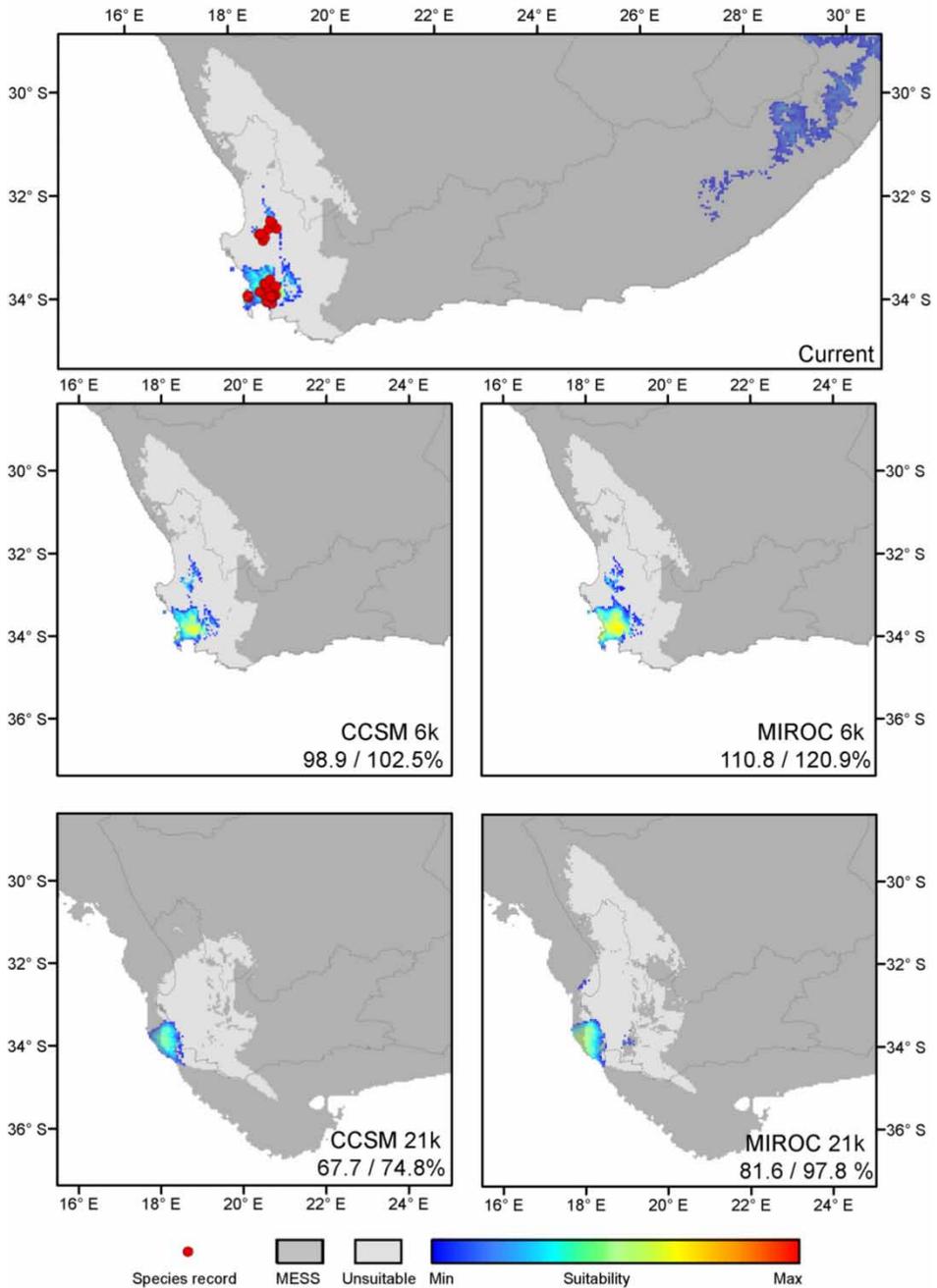
Hadromophryne natalensis



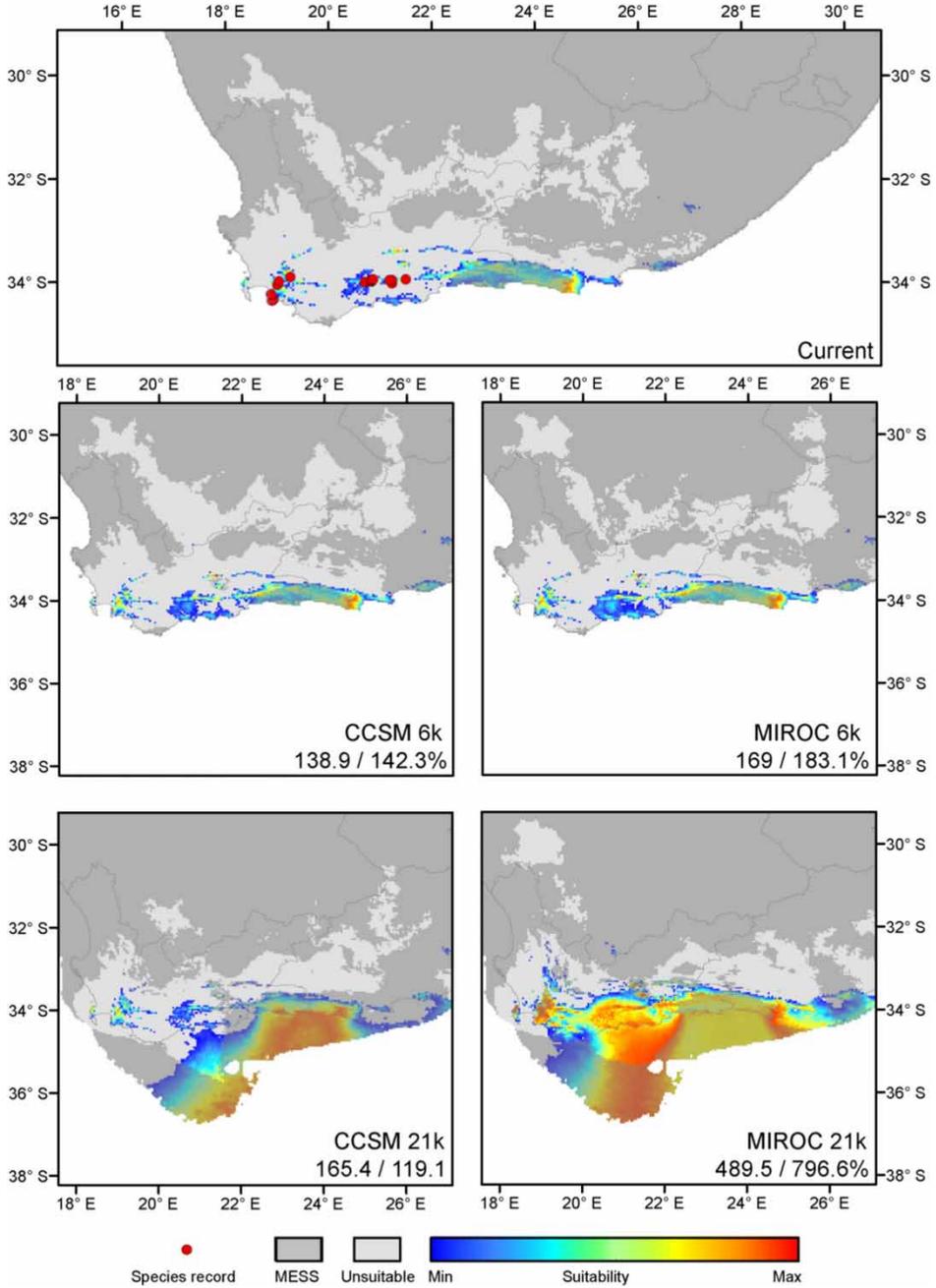
Cacosternum capense



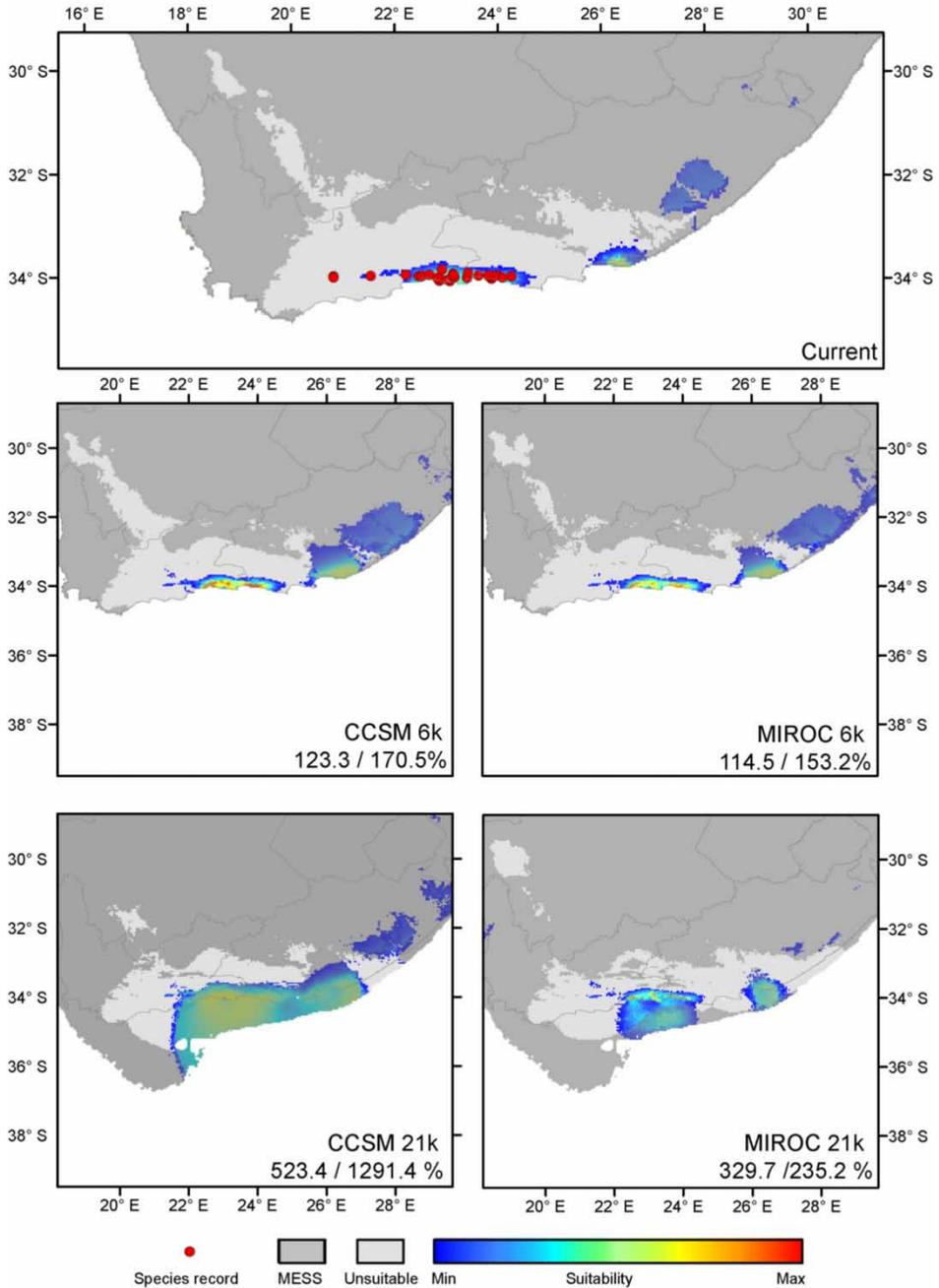
Breviceps gibbosus



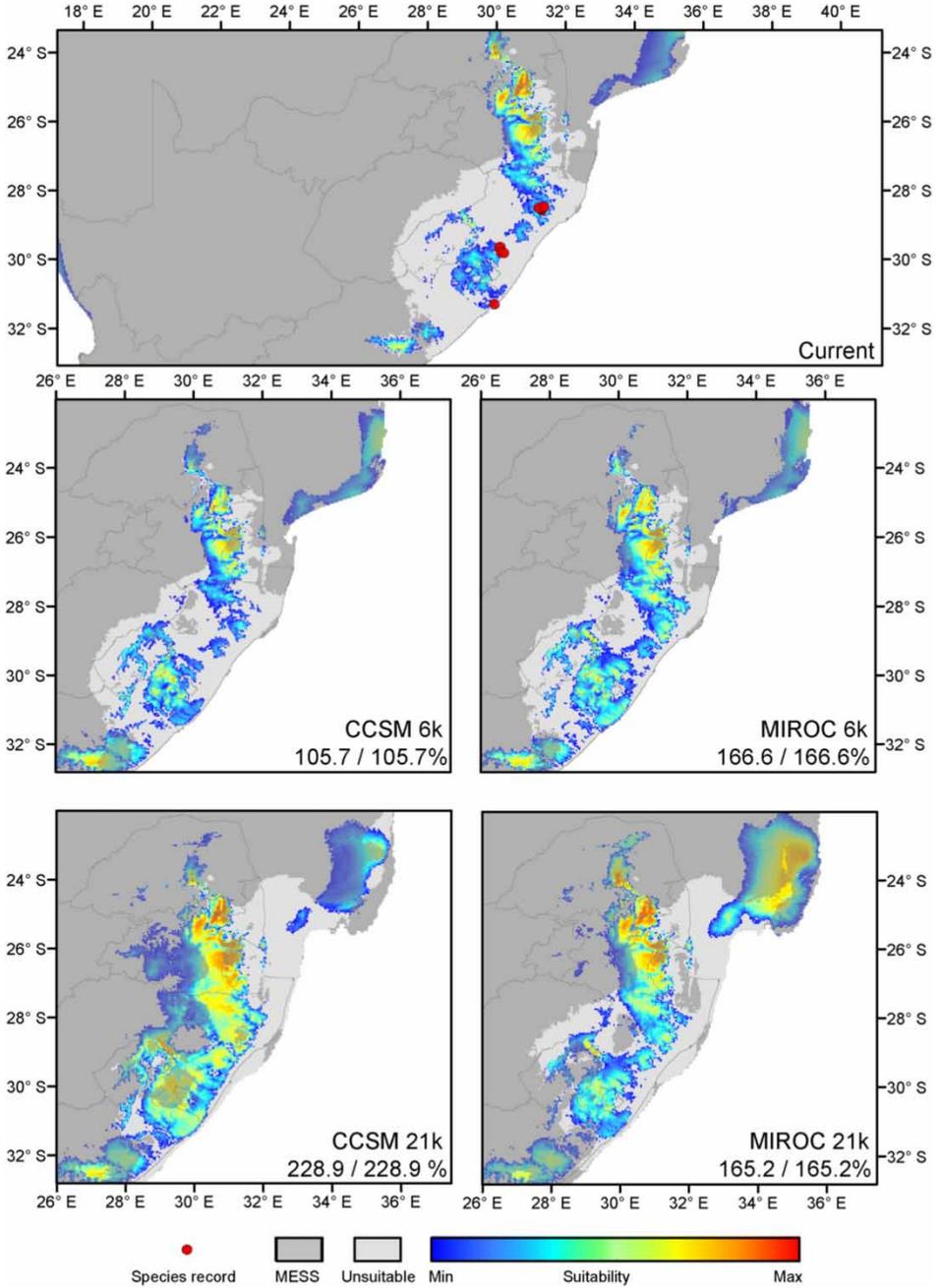
Breviceps acutirostris



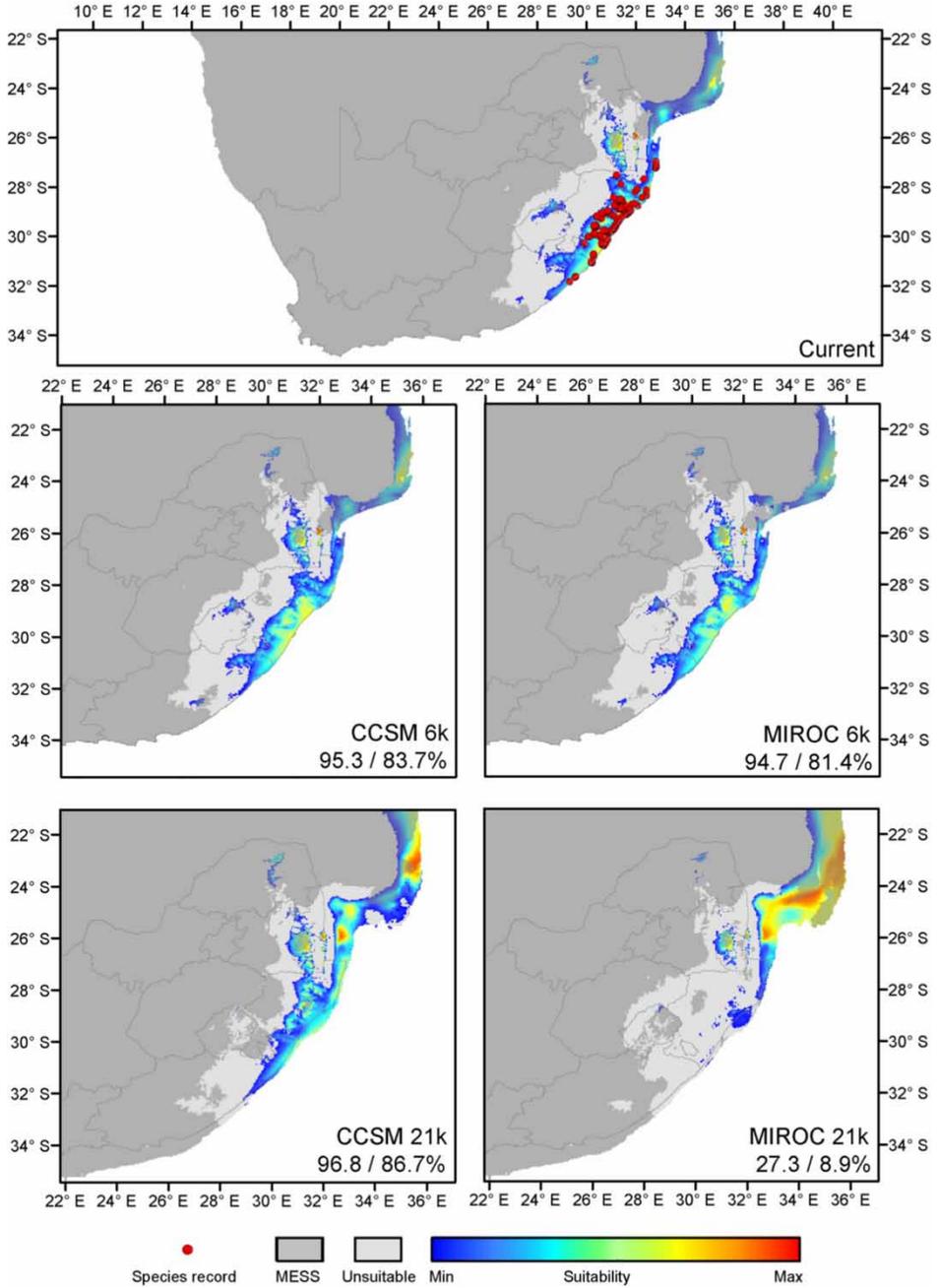
Breviceps fuscus



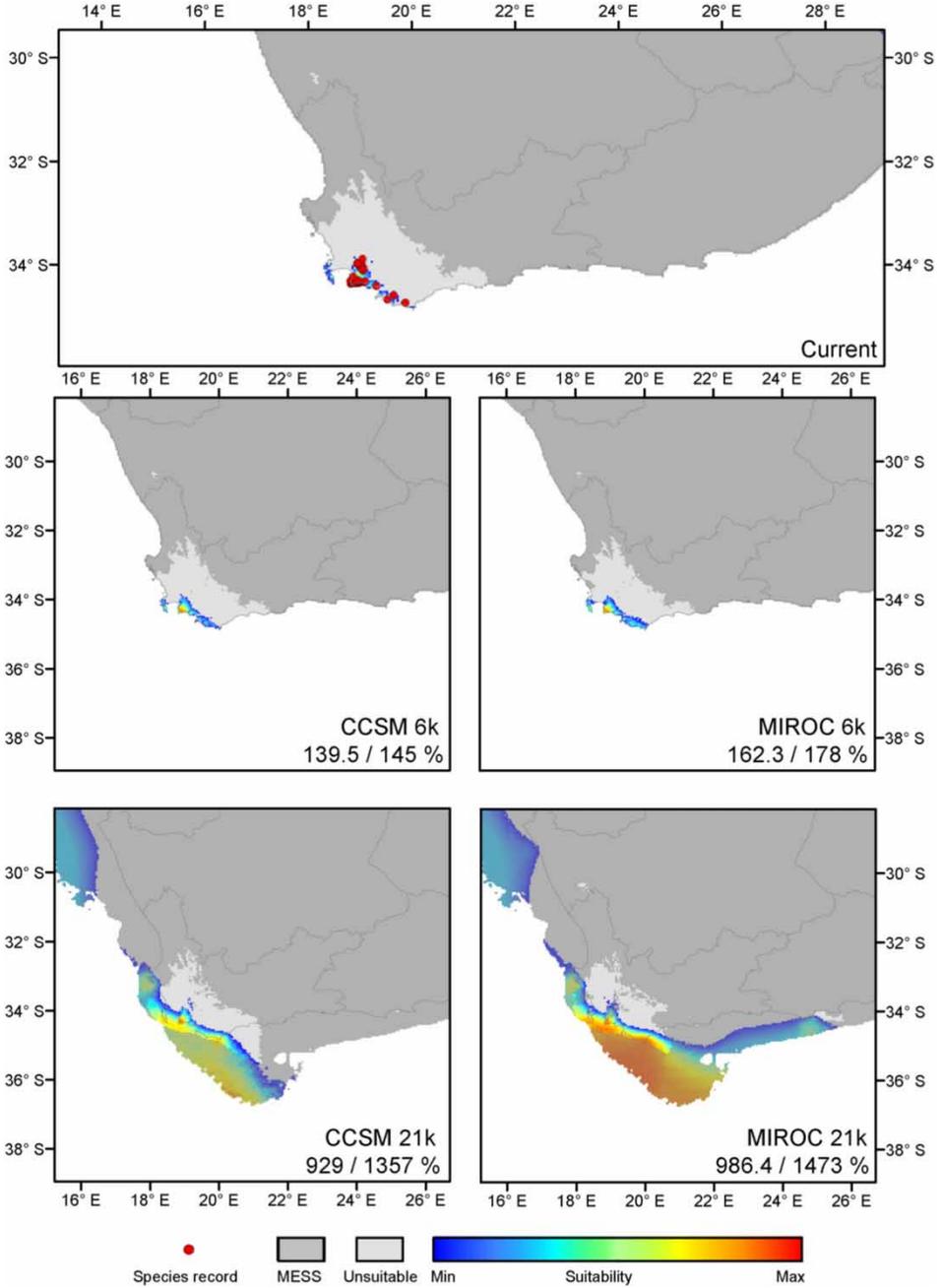
Breviceps bagginsi



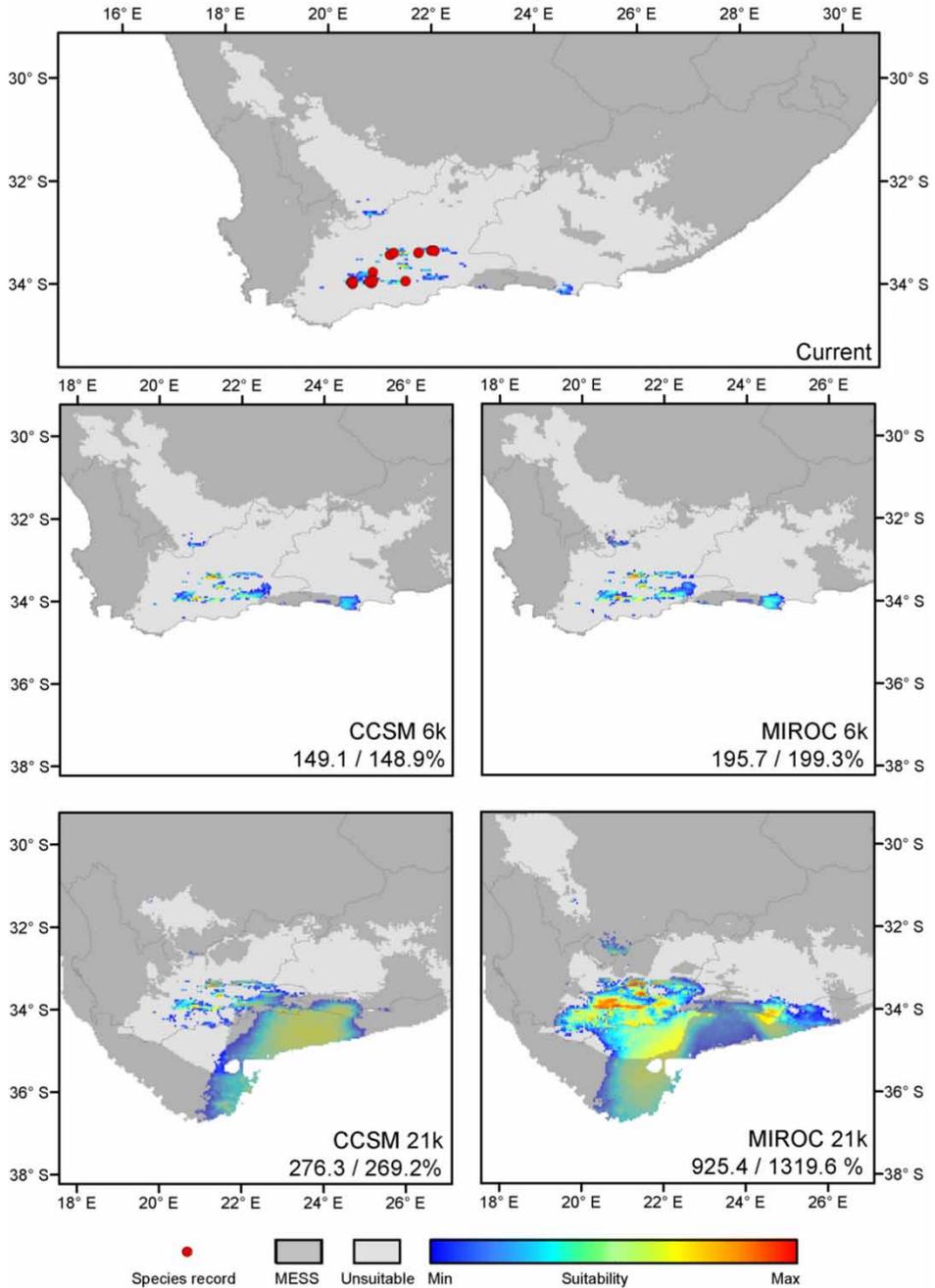
Arthroleptis wahlbergi



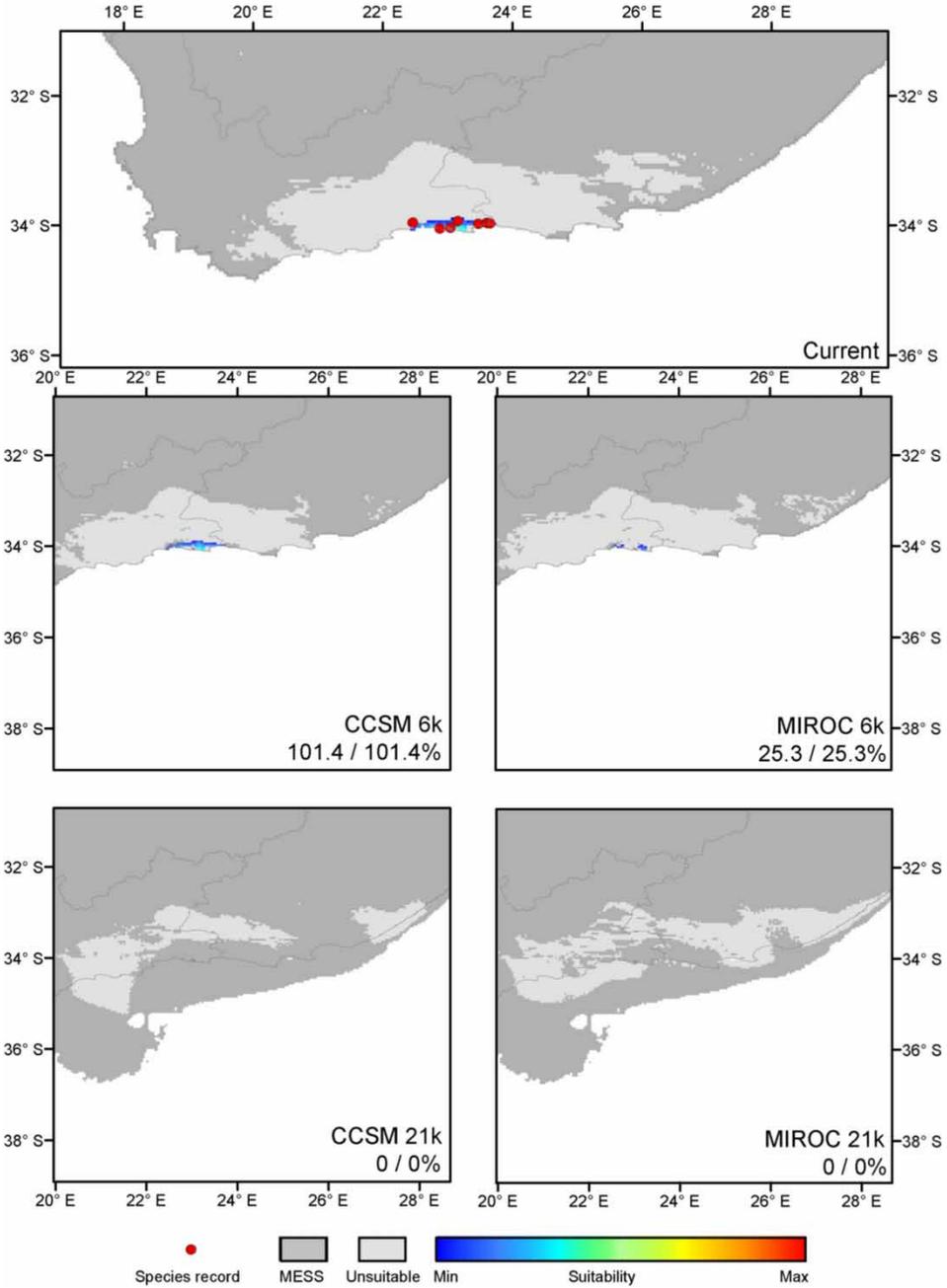
Arthroleptella villiersi



Amietia vandijki



Afrixalus knysnae



Xenopus gilli

