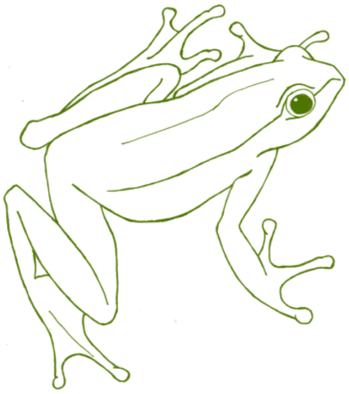

University of the Witwatersrand

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Distribution change in South African frogs

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

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Abstract

Range change is a common species response to global change. Comparing historical species distribution data with recent biological surveys has the potential to quantify changes to species geographic ranges. However, the broad-scale sampling strategies typically employed to acquire primary species distribution data are prone to errors of omission. The aim of this study was to evaluate the *South African Frog Atlas Project* (*SAFAP*) as a means for detecting changes in amphibian species distributions and to relate observed range changes to extrinsic environmental factors and intrinsic species characteristics. The *SAFAP* provided historical (1905 – 1995) and recent (1996 – 2003) species distributions of the amphibians of South Africa. Geographic sampling bias in the dataset was assessed by relating collection density and species richness to hypothesised sources of bias. Several methods for managing differing sampling intensity were tested on hypothetical ranges. The best methods were applied to the South African species to investigate range dynamics. Changes to the size of species ranges and shifts in mean range centre were assessed. An Ecological Niche Factor Analysis provided comparative measures of climate and habitat niche breadth for each species. *SAFAP* sampling was concentrated around cities, roads and protected areas, resulting in relatively overestimated species richness and range sizes near to these features. Large parts of the arid northwestern regions were under-sampled. An increase in sampling intensity over time resulted in the false detection of range expansions. The most reliable method to correct for increased sampling was a mathematical correction factor, according to which, 60.2% of South African frog species have undergone range contractions. Upslope shifts of 47.6 m were found for South African species and species of the Bushveld region shifted towards an area of Savanna Biome resilience. While several of the observed changes to species ranges were consistent with global change predictions, southern hemisphere amphibians may show a differing response to global change to that which is commonly predicted. Small range size, habitat specialisation and climate specialisation were significant predictors of range contractions for all species. Contracting habitat specialists were concentrated within two areas of endemism that also had high levels of land transformation. The use of methods that correct for sampling variation has allowed the *SAFAP* to be valuable in investigating species range change.

Declaration

I hereby declare that this Thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted for any degree or examination at any other University.

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Emily Anne Botts

14 September 2012, Johannesburg

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Chapter 1: Introduction

1.1. Amphibian declines as a component of global biodiversity loss

The Earth is at present immersed in a global biodiversity crisis, in which populations are declining and extinction risk is increasing (Chapin III et al., 2000; Butchard et al., 2010). Consequently, 33% of all the species evaluated in the latest Red Data list are classified as Threatened (IUCN, 2010). This is significant because the irrevocable loss of species may cause alterations to global biogeochemical processes, disturbance regimes, trophic interactions, ecosystem resilience and to the human benefits obtained from ecosystem goods and services (Chapin III et al., 2000). Parallel to this global biodiversity crisis is a corresponding global decline in amphibians. Global declines in amphibian populations were first observed in the 1980s, in particular through discussion at the First World Congress of Herpetology in 1989 (Phillips, 1990; Stuart et al., 2004). It soon became clear that amphibian populations in Australia and the America's were rapidly succumbing to some unknown threats (Phillips, 1990; Collins & Storfer, 2003). Since then, amphibian declines have been well documented, culminating in the Global Amphibian Assessment (GAA) released in 2004, and subsequently updated in 2008. The GAA was commissioned by the IUCN to evaluate the status of all amphibian species described worldwide. Findings showed that 30% of amphibian species are Threatened (IUCN, 2010) and that at least 43% of species are experiencing reductions in population size (Stuart et al., 2004; IUCN, Conservation International & NatureServe, 2008).

Amphibians appear to be at greater risk than either birds (12% Threatened) or mammals (21% Threatened) (Cushman, 2006; IUCN, 2010). Although habitat modification and overutilization are serious threats, many of the observed rapid population declines seem to show a new, global threat that is thus far inadequately described (Collins & Storfer, 2003; Stuart et al., 2004). It has been proposed that amphibians could be bio-indicators, representing ecosystem stress and forecasting biodiversity loss in other taxa (Blaustein & Kiesecker, 2002; Carey & Alexander, 2003; Collins & Storfer, 2003; Du Preez & Curruthers, 2009). Amphibians are especially sensitive for several reasons. They are ectothermic and certain physiological processes are affected by environmental temperatures (Carey & Alexander, 2003; Du Preez & Curruthers, 2009). Moist, permeable skin makes them vulnerable to both desiccation and contaminants (Blaustein & Kiesecker, 2002; Du Preez & Curruthers, 2009). In addition, their dual aquatic and terrestrial lifestyle exposes them to stressors in both these systems (Du Preez & Curruthers, 2009). If amphibians prove to be a precursor to similar declines in other taxa, it is necessary to understand how amphibians are responding to the current major threats.

Amphibians occupy a central trophic level; by being both predators and prey, they provide a link between aquatic and terrestrial ecosystems (Du Preez & Curruthers, 2009). Declines could thus have far reaching effects on ecosystem functioning and the provision of ecosystem goods and services. It is therefore necessary to understand the response of amphibians to changes in the environment and subsequently, identify those changes that could be implicated in population declines and eventual extinction. This will guide conservation efforts as well as improve theoretical knowledge of the response of species to anthropogenic changes to the environment.

1.2. Primary causes of amphibian declines

Collins and Storfer (2003) divided the hypothetical causes of amphibian declines into two major classes. Firstly, those factors that have been clearly causing species declines in many taxa for many years and for which the direct effects are evident. The most obvious of these factors is land-cover change. Even at a global scale, the impact of human-driven land-cover change is apparent. Humans have transformed a large proportion of the land surface of the earth, fragmenting most natural ecosystems (Vitousek et al., 1997; Chapin III et al., 2000; Ellis & Ramankutty, 2008). Fifty-four percent of all accessible fresh water is directly utilised by humans and many rivers are altered to make this water available (Vitousek, 1997). Habitat transformation has a dual impact for amphibians: upland habitat alteration affects connectivity, dispersal and resource availability for terrestrial adult stages (Cushman, 2006), while catchment transformation affects the timing, volume and quality of runoff important for breeding and aquatic life-stages (Tockner et al., 2010). According to the Global Amphibian Assessment, land-cover change is by far the biggest threat to amphibian species worldwide, with nearly 4 000 species adversely affected by habitat alterations (Stuart et al., 2004; IUCN, Conservation International & NatureServe, 2008).

The second class of threats is termed “enigmatic declines” by Stuart et al. (2004). Factors in this class have indirect or combined effects on populations, have emerged recently and are poorly understood (Collins & Storfer, 2003). The predominant factor in this class is the emergence and spread of the chytrid fungus *(Batrachochytrium dendrobatidis*) which can cause lethal morphological changes to a frog’s skin (Voyles et al., 2007), and has been implicated in many cases of rapid amphibian declines, particularly those in pristine habitats (Blaustein & Kiesecker, 2002; Minter et al., 2004; Voyles et al., 2007). In some cases, changes in environmental variables may increase the susceptibility of amphibians to chytrid fungus or promote optimum conditions for the spread of this pathogen (Blaustein & Dobson, 2006; Pounds et al., 2006). The declines and extinction of various Harlequin frogs (*Atelopus*) from South America have been correlated with an increase in the frequency of dry-days, which consequently caused changes in cloud cover that favoured the spread of the chytrid pathogen (Pounds et al., 1999; Blaustein & Dobson, 2006; Pounds et al., 2006). Either global warming, and/or severe El Niño (Anchukaitis & Evans, 2010) may be responsible for this series of events. Thus, climate is also considered a significant factor within this class of threats, although causal relationships between amphibian population changes and climate are difficult to elucidate (Carey & Alexander, 2003) and may be complex (Blaustein & Kiesecker, 2002). Global mean temperature has increased by 0.74 °C in the past century, with corresponding changes in precipitation and extreme weather events (IPCC, 2007). While few studies are able to show causative evidence of a species or community response to climate change, meta-analyses indicate that there is a definitive trend in both geographic range shift and phenological change that corresponds to expected climate change effects (McCarty, 2001; Parmesan & Yohe, 2003; Root et al., 2005; Rosenzweig et al., 2007).

Understanding how amphibians have responded to the current levels of environmental change will ensure that future conservation and mitigation efforts can be more effectively applied. Amphibian responses could also be precursory to similar responses in other taxa and will therefore have a bearing on biodiversity losses in general. Both of the major threats of land-cover and climate change can have an observable and quantifiable impact on the geographic range of species. This makes species distributions a useful measure of species decline in response to these threats (Shaffer et al., 1998; Joseph & Possingham, 2008).

1.3. Species range change in response to environmental threats

Areography describes the measurement of the size, shape, internal structure and location of a species range (Donald & Fuller, 1998). Accurate estimates of species areography are essential in biodiversity assessments and conservation planning. The dimensions of species ranges can also be correlated with environmental factors to provide information about their physiological limits, resource requirements and interspecific interactions (Brown et al., 1996). While snapshot areography can answer many questions about species biology and history, changes in areography over time reveal the dynamic nature of species ranges in response to environmental perturbations.

Amphibian distributions can be negatively impacted by land-cover change if individuals are killed, if resources are reduced, or if preferred habitat is destroyed or fragmented such that dispersal is prevented (Sih et al., 2000; Collins & Storfer, 2003; Cushman, 2006). The effects of land-cover change on species distributions are generally considered widespread and obviously apparent, although few studies have demonstrated the mechanistic processes by which amphibians respond to habitat modifications (Gardner et al., 2007). Species distributions often follow a similar spatial structure to underlying habitat elements (Pocock et al., 2006; Gardner et al., 2007). As such, the terms habitat loss, destruction, alteration and fragmentation express the varying intensity of land transformation and the consequent effects on amphibian species ranges (Sih et al., 2000; Blaustein & Kiesecker, 2002; Ficetola & De Bernardi, 2004; Cushman, 2006; Gardner et al., 2007; Sodhi et al., 2008).

When examining a species' range, the species response to land-cover change will be evident through the effects of local extinctions (Sih et al., 2000). These local extinctions will theoretically result in an irregular loss of range, spread throughout the species distribution, in regions where land transformation has been the most extensive (Donald & Fuller, 1998; Pocock et al., 2006). Most species experiencing land-cover alterations will be negatively affected and show patchy range contractions. In particular, habitat specialists and small-range species will usually decline as their preferred habitat is reduced (Pearson et al., 2004; Sodhi et al., 2008). The most resilient species will remain in transformed areas for longer (Ficetola & De Bernardi, 2004). Some may even benefit from certain land-cover changes, and expand their ranges accordingly (Cushman, 2006). These opportunistic generalist species take advantage of any available habitats and are able to exploit most resources (Fairbanks et al., 2002; Fairbanks, 2004).

Contrary to the local extinctions that result from land-cover change, the broader scale of climate change generally involves a shift in the entire distribution of a species (Donald & Fuller, 1998, Warren et al., 2001; Pearson et al., 2004). Range shifts are a common response to changing temperatures and precipitation, as species track optimal climate conditions through local dispersal and extinction events (Gaston, 2003; Hickling et al., 2005; Thomas, 2010). Under the present warming trend, there is evidence of poleward and up-slope movement of species (McCarty, 2001; Parmesan & Yohe, 2003; Root et al., 2003; Hickling et al., 2006; Rosenzweig et al., 2007). The pattern of range shift is often related to range boundaries (McCarty, 2001; Dennis & Shreeve, 2003; Thomas, 2010). The trailing edge of the range is either stable or contracts, while the opposite, leading edge expands (Hampe & Petit, 2005; Thomas, 2010). A latitudinal or altitudinal correlation to these shifts aids in the attribution of species range change to climate change. Taxa, such as amphibians, that are primarily climate limited and highly dependent on temperatures and water availability should show a consistent climate change response (Carey & Alexander, 2003; Hickling et al., 2005). Mobile, generalist species, which are already common and able to disperse to new areas, will show the fastest, and farthest range shifts (Pearson et al., 2004; Hickling et al., 2005; Thomas, 2010). Non-mobile species and species with slow reproductive cycles may not be able to track suitable climate and will show contraction of range (Pearson et al., 2004; Simmons et al., 2004; Hickling et al., 2005).

Thus, changes in the overall size and location of species ranges will provide evidence of species responses to a changing environment. Attribution of species responses to either land-cover or climate change threats will be enhanced by prior detection and quantification of species range changes.

1.4. Data requirements for quantifying range change

Recent concern over negative anthropogenic impacts on species has resulted in the re-evaluation of long-term, historical datasets and an increasing number of new biological atlases (Donald & Fuller, 1998; Ferrier et al., 2004; Graham et al., 2004; Rondinini et al., 2006; Boakes et al., 2010; Pyke & Ehrlich, 2010). A biological atlas is usually a grid-based, presence-only record of species occurrence for a taxonomic group in a specific region (Donald & Fuller, 1998; Dennis et al., 1999, Dunn & Weston, 2008; Robertson et al., 2010). Typically, it is conducted at a broader spatial scale than normal ecological investigations and combines records from several years of sampling (Donald & Fuller, 1998; Fairbanks et al., 2002). A complete atlas should theoretically provide the correct area of occupancy measurement for each species at the prescribed scale (Rondinini et al., 2006). The data made available via biological atlases have been useful in numerous different applications, from education of the public, to environmental impact assessments, to research directed at theoretical ecological questions (Donald & Fuller, 1998; Dunn & Weston, 2008; Robertson et al., 2010). For an assessment of range change, historical species distribution data from museums, literature and other archival sources is often compared with more recent datasets (Shaffer et al., 1998; McCollin et al., 2000; Telfer et al., 2002; Kuussaari et al., 2007; Pyke & Ehrlich, 2010; Robertson et al., 2010).

Since atlases are often the only available data to describe the geographic ranges of species, much emphasis has been placed on their limitations for this application (McCollin et al., 2000; Funk & Richardson, 2002; Telfer et al., 2002; Reddy & Dávalos, 2003; Tyre et al., 2003; Pressey, 2004; Robertson et al., 2010). Some researchers have questioned whether the time and capital invested in biological atlases is worth the outcomes that are produced (Lawes & Piper, 1998; Dennis et al., 1999). The grain of atlases is criticised for being too coarse to detect small-scale trends (Donald & Fuller, 1998; Shoo et al., 2006). Similarly, atlases combine records from many years, which may obscure the short-term dynamics of species ranges (Fairbanks et al., 2002; Rondinini et al., 2006). Atlases are particularly vulnerable to omission errors, which in turn introduce bias into the datasets (Williams et al., 2002; Tyre et al., 2003; Rondinini et al., 2006). Omission error (or false negative error) occurs when an organism or species is present in a sampling unit but is not recorded there (Williams et al., 2002; Tyre et al., 2003; Rondinini et al., 2006).

Geographic, or spatial, sampling bias refers to the case in which omission errors occur non-randomly in space. This occurs when certain areas are favoured during sampling and receive higher sampling intensity, while others are neglected (Funk & Richardson, 2002; Robertson & Barker, 2006; Rondinini et al., 2006). The location of records thus tends to follows roads, rivers, airfields, field stations, specialist institutions, protected areas, populated places and areas of perceived high biodiversity (Williams et al., 2002; Reddy & Dávalos, 2003; Pressey, 2004; Boakes et al., 2010). Conveniently-located areas that are easily accessed are generally better sampled. Higher sampling intensity occurs near to cities, which house the institutions and researchers responsible for specimen collection (Freitag et al., 1998; Parnell et al., 2003; Reddy & Dávalos, 2003; Romo et al., 2006; Ferreira et al., 2007; Pyke & Ehrlich, 2010). Similarly, common travel routes are often better sampled (Williams et al., 2002; Pyke & Ehrlich, 2010). In addition to conveniently accessible areas, collectors tend to favour areas that they presume will be rewarding or valuable for research (Williams et al., 2002; Reddy & Dávalos, 2003; Küper et al., 2006; Romo et al., 2006; Boakes et al., 2010). This includes protected areas and those areas known for high biodiversity.

Geographic sampling bias can affect the ability of data to be useful for achieving biogeographic and conservation goals. Spatial variation in sampling intensity can result in incorrect species richness and range size measures. Low sampling effort in a region can result in smaller documented range sizes and a consequent over-estimation of endemism (Küper et al., 2006). Areas that are poorly sampled often appear less species-rich than better-sampled areas (Reddy & Dávalos, 2003). The delineation of biogeographic units and the investigation of species-environment relationships are hampered by poor quality data (Brown et al., 1996; Donald & Fuller, 1998; Parnell et al., 2003; Graham et al., 2004; Küper et al., 2006). Conservation planning also requires accurate biodiversity and species distribution data for reserve selection procedures to be optimally applied (Freitag et al., 1998; Gaston & Rodrigues, 2003; Reddy & Dávalos, 2003). It is thus prudent to identify areas of low sampling intensity before conducting any study that requires the calculation of either species richness or range size.

Temporal irregularities in sampling can also hamper the comparisons between datasets from different time-periods. Such temporal sampling bias typically manifests as an increase in sampling intensity over time (Telfer et al., 2002; Dennis & Shreeve, 2003; Romo et al., 2006; Ferreira et al., 2007), due to the additional survey effort and resources utilised in the compilation of recent biological atlases. When sampling intensity is low, species tend to be recorded only in areas where they are locally abundant (Gaston & Rodrigues, 2003). Rare and restricted-range species are often overlooked altogether (Gaston & Rodrigues, 2003; Boakes et al., 2010; Robertson et al., 2010). Increasing sampling intensity can result in an increase in the total number of presence records (Romo et al., 2006; Ferreira et al., 2007), improved coverage of the study area (Ferreira et al., 2007), an apparent increase in species richness (Elphick, 1997; Dennis et al., 1999; Romo et al., 2006; Ferreira et al., 2007) and improved accuracy in correlations with environmental variables (Kodric-Brown & Brown, 1993; Tyre et al., 2003).

Critically for studies of range change over time, the measurement of species range size is also dependent on sampling intensity (Gaston & Rodrigues, 2003; Ferreira et al., 2007). Thus, comparing datasets with different sampling strategies (such as the comparison of recent atlases with historical museum data) may result in erroneous range change measures (Donald & Fuller, 1998; Shaffer et al., 1998; Tingley & Beissinger, 2009). If the sampling intensity for the second database is greater, the ranges of species may seem to be expanding (Ferreira et al., 2007; Shoo et al., 2006). Conversely, if the resurvey time is short, there may be an apparent contraction of species ranges (Skelly et al., 2003).

Therefore, any biogeographical study making use of either historical or atlas data must first provide a detailed account of the extent of sampling bias within the datasets used (Skelly et al., 2003; Romo et al., 2006; Reddy & Dávalos, 2007). If this evaluation is thoroughly conducted, then even biased data can be useful in identifying broad scale patterns in species distribution change and assessing hypothetical causes of this change (Donald & Fuller, 1998; Williams et al., 2002; Parnell et al., 2003; Romo et al., 2006). Several methods are available that allow datasets with differing sampling intensity to be more reliably used in range change comparisons (Van Swaay, 1990; Rich & Woodruff, 1996; Warren et al., 2001; Telfer et al., 2002; Kuussaari et al., 2007; Tingley & Beissinger, 2009; Boakes et al., 2010).

1.5. Range change in South African frogs

South Africa currently has 117 described species of anurans, divided among 13 families and 33 genera (Du Preez & Curruthers, 2009). Of these 117 species, just over half are endemic to South Africa, including one endemic family, the Heleophrynidae (Du Preez & Curruthers, 2009). Sixteen percent of South Africa's frogs are considered Threatened, but a further 9% are classified as either Near Threatened or Data Deficient (IUCN, 2010). The GAA also estimated the population trends of each frog species. For South African frogs, 20% were undergoing a decrease in population size, 2% were increasing and 54% were stable. The remaining 24% of species had unknown population trends (IUCN, Conservation International & NatureServe, 2008).

According to the global scale analysis of Stuart et al. (2004), the only threat to South African amphibians is reduction of habitat, which occurs along the eastern and southern coastlines. Undeniably, habitat destruction affects a large number South African frog species. All of the 20 Threatened species in South Africa are at risk from habitat loss (IUCN, Conservation International & NatureServe, 2008) and even those that are not Threatened may be negatively affected by changing land-cover (Minter et al., 2004). There are several different forms of land-cover change that occur in South Africa including afforestation, urban development, increasing agriculture, strip mining and the introduction of alien invasive vegetation, as well as the impoundment and extraction of water from rivers and wetlands (Minter et al., 2004).

Although the present biogeographic patterns of South African frog taxa are assigned primarily to past climatic changes (Alexander et al., 2004), distribution change due to current anthropogenic climate change has not been investigated. Global Circulation Models predict an approximate 1 – 4 °C increase in temperatures for southern Africa by 2080, depending on the emissions scenario (Kiker, 2000; Boko et al., 2007). In addition, precipitation is expected to show a 5 – 10% decrease in general (Kiker, 2000), and a 30% decrease during winter (Boko et al., 2007), although some areas may receive more rainfall.

The completion of the *South African Frog Atlas Project* (*SAFAP*) in 2004 opportunely coincided with the enhanced public and scientific interest in amphibian declines and biodiversity loss in general. The *SAFAP* was a project run by the Animal Demography Unit at the University of Cape Town. The project was initiated as a means to improve the quality of species distribution data available for South Africa amphibians (Minter et al., 2004). Twenty-eight universities and scientific institutions participated, either by supplying historical data or by contributing to active data collection (Minter et al., 2004). Volunteers and herpetologists contributed to active data collection between 1996 and 2003 by systematically surveying the majority of Quarter Degree Grid Cells (QDGCs) in South Africa, Lesotho and Swaziland. At each grid cell, presence records for frog species were entered onto report forms (Minter et al., 2004). The report forms and associated evidence were checked and processed by regional organisers before being sent to the University of Cape Town for data capture. Historical data were included to augment the data collected during the atlas survey. Museums, personal databases and the literature record were used as sources for historical data that covered approximately 100 years of sampling (Minter et al., 2004). Data were corrected for up-dated taxonomic classifications and doubtful records were excluded. Ultimately, 16 983 historical records were included to support the 25 486 records collected during the atlas period.

1.6. Project statement: Aims, Objectives and Hypotheses

Assumptions of poor data quality have resulted in limited use of the *SAFAP* in biogeographical or macroecological research. The lack of any measure of sampling effort means that true absences cannot be easily distinguished from non-detections, leaving possible sampling biases unknown. However, the extent of this shortcoming has not been explored. Like previous southern African atlases, the *SAFAP* dataset may prove to be a valuable source of information on the spatial distribution of species (Dunn & Weston, 2008; Harrison et al., 2008).

This project is the first independent comprehensive assessment of the *South African Frog Atlas Project*. The *SAFAP* is the supporting database for an analysis of the range dynamics of South African amphibians. Quantifying range changes for South African frogs will contribute to understanding of the response of species to anthropogenic environmental threats, both within South Africa and within the broader global context.

Therefore, the aims and objectives are:

1.6.1. *Aim*

To evaluate the *South African Frog Atlas Project* as a means for detecting changes in amphibian species distributions and to relate observed range changes to extrinsic environmental factors and intrinsic species characteristics.

1.6.2. *Objective 1*

To perform an assessment of geographic sampling bias within the South African Frog Atlas data.

Hypothesis 1.1: There is an inequality in geographic sampling intensity over the study area, with the number of records differing between QDGCs, resulting from a combination of real patterns in species distribution as well as sampling bias.

Hypothesis 1.2: There is a greater intensity of sampling in the proximity of roads, cities, scientific institutions and similar places allowing ease of access for sampling.

Hypothesis 1.3: There is a greater intensity of sampling in the proximity of protected areas, due to perceived higher biodiversity.

Hypothesis 1.4: Estimates of species richness are higher in regions with higher sampling intensity, as additional records result in higher detection probabilities.

1.6.3. *Objective 2*

To identify a method for calculating reliable range change estimates for South African amphibians while accounting for sampling biases in the *South African Frog Atlas Project* data.

Hypothesis 2.1: There is improved geographic coverage of the study area and increased sampling intensity between the historical and atlas datasets of the *SAFAP*.

Hypothesis 2.2: Increased sampling intensity between the historical and atlas datasets of the *SAFAP* will result in erroneous increases in the measured size of species ranges.

Hypothesis 2.3: Accounting for improved geographic coverage and increased sampling intensity will allow for estimates of range size change that are more reliable.

Hypothesis 2.4: Similar proportions of South African amphibians are experiencing range contractions as the global estimates (43% declining).

1.6.4. *Objective 3*

To relate observed range dynamics of South African frog species to theoretical land-cover and/or climate change predictions.

Hypothesis 3.1: The percentage of South African amphibians experiencing declines (range contractions) is similar to the estimated global average of 43%.

Hypothesis 3.2: Shifts in species ranges show consistency with global or local climate change predictions.

Hypothesis 3.3: Species belonging to the same biogeographic district show similar range change responses to anthropogenic global change.

1.6.5. *Objective 4*

To calculate a relative measure of niche breadth for South African amphibian species and test whether niche breadth is a significant correlate of observed declines.

Hypothesis 4.1: Niche breadth can be reliably documented using the *SAFAP* dataset despite sampling biases.

Hypothesis 4.2: Species with narrow niche breadth have experienced greater range contractions than have species with wide niches.

Hypothesis 4.3: Habitat specialists with contracting ranges are located in regions with high land transformation.

Each of the four objectives is presented as an independent, publishable paper. As such, there is some repetition of the contextual information. I am the first author of all four papers, and performed all of the data analysis and initial writing. My supervisors co-authored each paper and contributed to initial conceptualisation, data acquisition and subsequent editorial improvements of the manuscripts. Chapter 2 contains the first paper dealing with the geographic sampling bias hypotheses of Objective 1. This paper has already been published in the journal *Biodiversity and Conservation*. The paper presented in Chapter 3 reports on the evaluation of range change methods for Objective 2 and has been published in *Biological Conservation*. The paper in Chapter 4 addresses the hypotheses of Objective 3, relating range shifts to land-cover or climate change predictions. This paper is currently under review. Chapter 5 contains the final paper investigating the niche breadth hypotheses of Objective 4. This paper has been accepted for publication in *Global Ecology and Biogeography* and is currently in press.

1.7. References

Alexander, G. J., Harrison, J. A., Fairbanks, D. H. & Navarro, R. A. (2004) Biogeography of the Frogs of South Africa, Lesotho and Swaziland. In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H.H., Bishop, P. J. & Kloepfer, D. (eds) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

Anchukaitis, K. J. & Evans, M. N. (2010) Tropical cloud forest climate variability and the demise of the Monteverde golden toad. *Proceedings of the National Academy of Sciences* 107: 5036-5040.

Blaustein, A. R. & Kiesecker, J. M. (2002) Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters* 5: 597-608.

Blaustein, A. R. & Dobson, A. (2006) A message from the frogs. *Nature* 439: 143-144.

Boakes, E. H., McGowan, P. J. K., Fuller, R. J., Chang-qing, D., Clark, N. E., O'Connor, K. & Mace, G. M. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8: e1000385.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, M., Osman-Elasha, B., Tabo, R. & Yanda, P. (2007) Africa. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C.E. (eds) Cambridge University Press, Cambridge, UK, 433-467.

Brown, J. H., Stevens, G. C. & Kaufman, D. M. (1996) The Geographic Range: Size, Shape, Boundaries, and Internal Structure. *Annual Review of Ecology and Systematics* 27: 597-623

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J. F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vié, J. C. & Watson, R. (2010) Global Biodiversity: Indicators of Recent Declines. *Science* 328: 1164-1168.

Carey, C. & Alexander, M. A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9: 111-121.

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. & Díaz, S. (2000) Consequences of changing biodiversity. *Nature* 405: 234-242.

Collins, J. P. & Storfer, A. (2003) Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9: 89-98.

Cushman, S. A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.

Dennis, R. L. H., Sparks, T. H. & Hardy, P. B. (1999) Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Dennis, R. L. H. & Shreeve, T. G. (2003) Gains and losses of French butterflies: tests of predictions, under-recording and regional extinction from data in a new atlas. *Biological Conservation* 110: 131-139.

Donald, P. F. & Fuller, R. J. (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study* 45: 129-145.

Dunn, A. M. & Weston, M. A. (2008) A review of terrestrial bird atlases of the world and their application. *Emu* 180: 42-67.

Du Preez, L. & Curruthers, V. (2009) *A complete guide to the frogs of southern Africa.* Struik Nature, Cape Town, South Africa.

Ellis, E. C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6: 439-447.

Elphick, C. S. (1997) Correcting avian richness estimates for unequal sample effort in atlas studies. *Ibis* 139: 189-190.

Fairbanks, D. H. K., Kshatriya, M., Van Jaarsveld, A. S. & Underhill, L. G. (2002) Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* 5: 61-73.

Fairbanks, D. H. K. (2004) Regional land-use impacts affecting avian richness patterns in Southern Africa-insights from historical avian atlas data. *Agriculture, Ecosystems and Environment* 101: 269-288.

Ferreira, D., Malard, F., Dole-Olivier, M.-J. & Gilbert, J. (2007) Obligate groundwater fauna of France: diversity patterns and conservation implications. *Biodiversity and Conservation* 16: 567-596.

Ferrier, S., Powell, G. V. N., Richardson, K. S., Manion, G., Overton, J. M., Allnutt, T. F., Cameron, S. E., Mantle, K., Burgess, N. D., Faith, D. P., Lamoreux, J. F., Kier, G., Hijmans, R. J., Funk, V. A., Cassis, G. A., Fisher, B. L., Flemons, P., Lees, D., Lovett, J. C. & Van Rompaey, R. S. A. R. (2004) Mapping More of Terrestrial Biodiversity for Global Conservation Assessment. *BioScience* 54: 1101-1109.

Ficetola, G. F. & De Bernardi, F. (2004) Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. *Biological Conservation* 119: 219-230.

Freitag, S., Hobson, C., Biggs, H. C. & Van Jaarsveld, A. S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Animal Conservation* 1: 119-127.

Funk, V. A. & Richardson, K. S. (2002) Systematic Data in Biodiversity Studies: Use It or Lose It. *Systematic Biology* 51: 303-316.

Gardner, T. A., Barlow, J. & Peres, C. A. (2007) Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation* 138: 166-179.

Gaston, K. J. (2003) Chapter 2: Range Edges. In: *The structure and dynamics of geographic ranges.* Oxford University Press, 20-65.

Gaston, K. J. & Rodrigues, A. S. L. (2003) Reserve Selection in Regions with Poor Biological Data. *Conservation Biology* 17: 188-195.

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C. & Townsend Peterson, A. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19: 497-503.

Hampe, A. & Petit, R. J. (2011) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8: 461-467.

Harrison, J. A., Underhill, L. G. & Barnard, P. (2008) The seminal legacy of the Southern African Bird Atlas Project. *South African Journal of Science* 104: 82-84.

Hickling, R., Roy, D. B., Hill, J. K. & Thomas, C. D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.

IUCN (2010) IUCN Red List of Threatened Species. Version 2010.4. http://www.iucnredlist.org. Cited 24 January 2011.

IUCN, Conservation International and NatureServe (2008) 2008 IUCN Red List www.iucnredlist.org/amphibians. Cited 18 October 2010.

IPCC (2007) Climate Change 2007: Synthesis Report. *Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C.E. (eds) Cambridge University Press, Cambridge, UK.

Joseph, L. N. & Possingham, H. P. (2008) Grid-based monitoring methods for detecting population declines: Sensitivity to spatial scale and consequences of scale correction. *Biological Conservation* 141: 1868-1875.

Kiker, G.A. (compiler) (2000) South African Country Study on Climate Change: Synthesis Report for the Vulnerability and Adaptation assessment section. In: Kiker, G.A., *Climate Change Impacts in Southern Africa. Report to the National Climate Change Committee*. Department of Environmental Affairs and Tourism, Pretoria, South Africa. http://www.sanbi.org/countrystudy/main.htm. Cited 24 October 2007.

Kodric-Brown, A. & Brown, J. H. (1993) Incomplete Data Sets in Community Ecology and Biogeography: A Cautionary Tale. *Ecological Applications* 3: 736-742.

Küper, W., Sommer, J. H., Lovett, J. C. & Barthlott, W. (2006) Deficiency in African plant distribution data – missing pieces of the puzzle. *Botanical Journal of the Linnean Society* 150: 355-368.

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation* 11: 351-366.

Lawes, M. J. & Piper, S. E. (2009) There is less to binary maps than meets the eye: The use of species distribution data in the southern African sub-region. *South African Journal of Science* 94: 207-210.

McCarty, J. P. (2001) Ecological Consequences of Recent Climate Change. *Conservation Biology* 15: 320-331.

McCollin, D., Moore, L. & Sparks, T. H. (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation* 92: 249-263.

Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H., Bishop, P. J. & Kloepfer, D. (eds) (2004) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Parnell, J. A. N., Simpson, D. A., Moat, J., Kirkup, D. W., Chantaranothai, P., Boyce, P. C., Bygrave, P., Dransfield, S., Jebb, M. H. P., Macklin, J., Meade, C., Middleton, D. J., Muasya, A. M., Prajaksood, A., Pendry, C. A., Pooma, R., Suddee, S. & Wilkin, P. (2003) Plant collecting spread and densities: their potential impact on biogeographical studies in Thailand. *Journal of Biogeography* 30: 193-209.

Pearson, R. G., Dawson, T. P. & Liu, C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27: 285-298.

Phillips, K. (1990) Where Have All the Frogs and Toads Gone? *BioScience* 40: 422-424.

Pocock, M. J. O., Hartley, S., Telfer, M. G., Preston, C. D. & Kunin, W. E. (2006) Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology* 94: 581-596.

Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. (1999) Biological response to climate change on a tropical mountain. *Nature* 398: 611-615.

Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sánchez-Azofeifa, G. A., Still, C. J. & Young, B. E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439: 161-167.

Pressey, R. (2004) Conservation Planning and Biodiversity: Assembling the Best Data for the Job. *Conservation Biology* 18: 1677-1681.

Pyke, G. H. & Ehrlich, P. R. (2010) Biological collection and ecological/environmental research: a review, some observations and a look to the future. *Biological Reviews* 85: 247-266.

Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography* 30: 1719-1727.

Rich, T. C. G. & Woodruff, E. R. (1996) Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217-229.

Robertson, M. P. & Barker, N. P. (2006) A technique for evaluating species richness maps generated from collections data. *South African Journal of Science* 102: 77-84.

Robertson, M. P., Cumming, G. S. & Erasmus, B. F. N. (2010) Getting the most out of atlas data. *Diversity and Distributions* 16: 363-375.

Romo, H., García-Barros, E. & Lobo, J. M. (2006) Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29: 873-885.

Rondinini, C., Wilson, K. A., Biotani, L., Grantham, H. & Possingham, H. P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136-1145.

Root, T. L., MacMynowski, D. P., Mastrandrea, M. D. & Schneider, S. H. (2005) Human-modified temperatures induce species changes: Joint attribution. *Proceedings of the National Academy of Sciences* 102: 7465-7469.

Rosenzweig, C., Casassa, G., Karoly, D. J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T. L., Seguin, B. & Tryjanowski, P. (2007) Assessment of observed changes and responses in natural and managed systems. (79–131) In: Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C. E. (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK.

Shaffer, H. B., Fisher, R. N. & Davidson, C. (1998) The role of natural history collections in documenting species declines. *Trends in Ecology and Evolution* 13: 27-30.

Shoo, L. P., Williams, S. E. & Hero, J.-M. (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology* 31: 22-29.

Sih, A., Jonsson, B. G. & Luikard, G. (2000) Habitat loss: ecological, evolutionary and genetic consequences. *Trends in Ecology and Evolution* 15: 132-134.

Simmons, R. E., Barnard, P., Dean, W. R. J., Midgley, G. F., Thuiller, W. & Hughes, G. O. (2004) Climate change and birds: perspectives and prospects from southern Africa. *Ostrich* 75: 295-308.

Skelly, D. K., Yurewics, K. L., Werner, E. E. & Relyea, R. A. (2003) Estimating Decline and Distributional Change in Amphibians. *Conservation Biology* 17: 744-751.

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H. & Bradshaw, C. J. A. (2008) Measuring the Meltdown: Drivers of Global Amphibian Extinction and Decline. *PLoS ONE* 3: 1-8.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. *Science* 306: 1783-1786.

Telfer, M. G., Preston, C. D. & Rothery, P. (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation* 107: 99-109.

Thomas, C. D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions* 16: 488-495.

Tingley, M. W. & Beissinger, S. R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution* 24: 625-633.

Tockner, K., Pusch, M., Borchardt, D. & Lorang, M. S. (2010) Multiple stressors in coupled river-floodplain ecosystems. *Freshwater Biology* 55 (S1): 135-151

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K. & Possingham, H. P. (2003) Improving Precision and Reducing Bias in Biological Surveys: Estimating False-Negative Error Rates. *Ecological Applications* 13: 1790-1801.

Van Swaay, C. A. M. (1990) An assessment of the changes in butterfly abundance in the Netherlands during the 20th Century. *Biological Conservation* 52: 287-302.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) Human Domination of Earth's Ecosystems. *Science* 277: 494-499.

Voyles, J., Berger, L., Young, S., Speare, R., Webb, R., Warner, J., Rudd, D., Campbell, R. & Skerratt, L. F. (2007) Electrolyte depletion and osmotic imbalance in amphibians with chytridiomycosis. *Diseases of Aquatic Organisms* 77: 113-118.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.

Williams, P. H., Margules, C. R. & Hilbert, D. W. (2002) Data requirements and data sources for biodiversity priority area selection. *Journal of Bioscience* 27: 327-338.

Chapter 2: Geographic sampling bias

Botts, E. A., Erasmus, B. F. N. and Alexander, G. J. (2011) Geographic sampling bias in the *South African Frog Atlas Project*: implications for conservation planning. *Biodiversity and Conservation* 20: 119-139, http://www.springerlink.com/content/atw38171535673g1/

2.1. Introduction

Recent concern over negative anthropogenic impacts on species and ecosystems has resulted in many studies detailing the necessity for large-scale, effective and timely conservation planning (Eken et al., 2004; Ferrier et al., 2004). Conservation planning requires primary input data, the optimal nature of which is still debated in the literature. In the absence of comprehensive species richness data, some authors have proposed the use of surrogates and proxies i.e. land cover types or 'indicator' species (see Funk & Richardson, 2002; Ferrier et al., 2004; Pressey, 2004; Larsen et al., 2009a). However, research has shown that surrogates perform poorly in regions where the spatial pattern of biodiversity differs among taxa (Van Jaarsveld et al., 1998a; Margules & Pressey, 2000; Pressey, 2004). Thus, most authors agree that robust conservation planning would benefit from accurate and current species distribution data for a wide variety of taxa (Donald & Fuller, 1998; Van Jaarsveld et al., 1998a; Ferrier, 2002; Pressey, 2004; Larsen et al., 2009a; Boakes et al., 2010).

This has consequently given rise to an increasing number of new biological atlases (Elphick, 1997; Donald & Fuller, 1998; Rondinini et al., 2006). A biological atlas is usually a grid-based, presence-only record of species occurrence for a specific taxonomic group, region and time scale (Donald & Fuller, 1998; Dennis et al., 1999; Dunn & Weston, 2008; Robertson et al., 2010). The *South African Frog Atlas Project* (*SAFAP*) is one such atlas with potential for inclusion in conservation plans. Atlases often offer the only broad-scale, current and spatially contiguous data available for conservation assessments; but their limitations for these applications are still much emphasised (McCollin et al., 2000; Funk & Richardson, 2002; Telfer et al., 2002; Reddy & Dávalos, 2003; Tyre et al., 2003; Pressey, 2004; Robertson et al., 2010). Atlases are particularly vulnerable to omission error, which in turn introduces bias to the datasets. False-negative error (or omission error) occurs when an organism or species is present but is not recorded (Williams et al., 2002; Tyre et al., 2003; Rondinini et al., 2006). Atlases should, in principle, be immune to such issues as they are systematic and aim to cover an area completely and thoroughly. However, in reality, atlases are subject to geographic bias due to logistical, budgetary and time constraints (Donald & Fuller, 1998; Robertson et al., 2010).

Geographic, or spatial, sampling bias refers to the case in which omission errors occur non-randomly in space. This arises when certain areas are favoured during sampling, thus receiving greater sampling intensity, and others are neglected (Funk & Richardson, 2002; Robertson & Barker, 2006; Rondinini et al., 2006).

The nature of false-negative error means that the bias in atlases is often predictable: higher sampling intensity in accessible areas or those favoured by researchers (Freitag et al., 1998; Funk & Richardson, 2002; Parnell et al., 2003; Reddy & Dávalos, 2003; Robertson & Barker, 2006; Romo et al., 2006; Ferreira et al., 2007). It has been shown that conveniently located areas are better-sampled (Freitag et al., 1998; Parnell et al., 2003; Reddy & Dávalos, 2003). In Thailand, there were many more plant records than expected within 4 km of populated places (Parnell et al., 2003). Records of passerine birds in sub-Saharan Africa were significantly closer to cities, rivers and roads than random (Reddy & Dávalos, 2003). Areas within an easy-access distance of populated places or common travel routes are therefore predicted to have higher sampling intensity due to greater accessibility.

In addition to conveniently accessible areas, collectors tend to favour areas that they presume will be rewarding or valuable for research (Williams et al., 2002; Reddy & Dávalos, 2003; Küper et al., 2006; Romo et al., 2006; Boakes et al., 2010). This includes protected areas and those areas already known for high biodiversity. This phenomenon has been termed 'diversity tracking' (Romo et al., 2006). On mainland Thailand, the three provinces with the highest plant collection density were those associated with national parks (Parnell et al., 2003). The correlation between one-degree grid cells containing protected areas and sampling of passerine birds in Africa was high ($R^2 = 0.74$; Reddy & Dávalos, 2003). Both Iberian butterflies (Romo et al., 2006) and plants in Thailand (Parnell et al., 2003) were better sampled in mountainous regions as these are the preferred study areas of researchers in an otherwise transformed landscape.

Variation in sampling intensity in space can result in incorrect species richness and distribution measures. Higher sampling intensity results in a higher probability of species detection (Elphick, 1997; Williams et al., 2002). Thus, well-sampled areas appear to be more species rich than poorly sampled areas (Reddy & Dávalos, 2003). Remote, poorly sampled regions will appear to have low species richness and will consequently be erroneously excluded from conservation plans (Reddy & Dávalos, 2003; Küper et al., 2006). These areas then appear of little scientific or conservation interest and continue to attract few researchers (Reddy & Dávalos, 2003; Küper et al., 2006). Conversely, planners will consider the placement of existing reserves particularly effective since high sampling intensity in these areas results in overestimated biodiversity (Freitag et al., 1998; Reddy &

Dávalos, 2003). Seemingly high diversity near to populated places also increases conflict between conservation and human development (Küper et al., 2006; Romo et al., 2006). Low sampling effort can result in smaller documented range sizes (Gaston & Rodrigues, 2003; Küper et al., 2006; Ferreira et al., 2007). It is thus prudent to identify areas of low sampling intensity before performing any conservation planning exercise.

The biodiversity information captured in biological atlases is usually incorporated into systematic conservation plans in the form of species distribution maps. These distribution maps can take a number of forms (Rondinini et al., 2006). They can simply be the unprocessed grid cell maps that are commonly the product of atlas projects. Alternatively, they can be generalised into interpreted distribution maps that display the broad areas in which species occur within the study area. This manipulation aims to reduce the frequent omission errors found in atlas data (Rondinini et al., 2006). Modelled distribution maps are occasionally included, often also with the intention of managing uncertainty and reducing omission error (Margules & Pressey, 2000; Funk & Richardson, 2002). Sometimes only species of special interest are included: rare, threatened or endemic species (e.g. Rouget et al., 2004). Some conservation plans use expert consultation to combine this information into areas of concern for a specific taxon. Locations with high endemism or high numbers of endangered species are thus included as biodiversity features (e.g. Desmet et al., 2008).

Once the biodiversity features have been mapped, specific targets are set which are defensible and quantitative (Margules & Pressey, 2000; Desmet & Cowling, 2004). These targets can range from a single occurrence of each species (e.g. Rouget et al., 2004) to 100% of the distribution in cases of Critically Endangered species (e.g. Ferrar & Lötter, 2007). Algorithms are then used to identify areas which can achieve the targets while minimising costs and maximising complementarity (Margules & Pressey, 2000). The result is a map of irreplaceability, in which planning units that are very important for meeting the targets are highly irreplaceable (Margules & Pressey, 2000).

Previous atlas projects in the southern African region have been extensively used in conservation planning exercises (Van Jaarsveld et al., 1998b; Larsen et al., 2009b), despite limitations of resolution, taxonomy, geographic coverage and bias. Indeed, conservation planning has been one of the major uses of the pioneering *South African Bird Atlas Project*, completed in 1997 (Dunn & Weston, 2008; Harrison et al., 2008). Similarly, both national and provincial conservation planning efforts have already made use of the *SAFAP* (Harrison et al., 2004). The South African National Spatial Biodiversity Assessment used the *SAFAP* for distribution data and conservation status of 11 Threatened frog species (Rouget et al., 2004). This assessment regarded the *SAFAP* as one of the better datasets available and largely exempted it from acknowledged biases due to systematic sampling (Rouget et al., 2004). The *SAFAP* has also been used in several regional conservation assessments (e.g. GDACE, 2004; Turner & De Villiers, 2007), although in these cases the Quarter Degree Grid Cell scale is often too coarse a resolution and only those records with accurate GPS positions can be included (57% of the total records). Most of these conservation planning efforts concede that bias-associated data may be limiting, but rarely quantify the degree of bias.

The editors of the *SAFAP* clearly acknowledge that geographic bias was present within the atlas data. Two specific restrictions were identified: arid and mountainous regions (Minter et al., 2004). Dry weather in the arid northwestern part of South Africa meant that trips to this region resulted in few records. In some cases, a visit to a grid cell returned no frog records. Thus, trips to this part of the country were targeted at the larger Half Degree Grid Cell (HDGC) scale to save money and time (Minter et al., 2004). Difficulty in accessing mountain peaks resulted in limited sampling in the Cape Fold Mountains, Drakensberg Mountains and mountainous areas of Lesotho (Minter et al., 2004).

In this paper, we provide a quantitative measure of geographic bias to inform accuracy assessment of conservation prioritisation efforts based on the *SAFAP*. We also include a parallel assessment of geographic bias within South African species distribution data available from the Global Amphibian Assessment (GAA), a possible alternative to the *SAFAP*. We evaluate the advantages and limitations of these data for use in conservation planning.

2.2. Methods

2.2.1. *The South African Frog Atlas data*

The *South African Frog Atlas Project* (*SAFAP*) was a project managed by the University of Cape Town's Animal Demography Unit (Minter et al., 2004). The project was initiated to improve the quality of the distribution data available for South African amphibians (Minter et al., 2004). Twenty-eight universities and scientific institutions participated in the frog atlas project, either by supplying historical data or by contributing to active data collection (Minter et al., 2004).

The atlas data were collected between 1996 and 2003 by volunteers and herpetologists who entered species information onto report forms (Minter et al., 2004). The report forms and associated evidence were checked and processed by regional organisers before being sent to the University of Cape Town for data capture. The methodology involved the systematic survey of the majority the Quarter Degree Grid Cells (QDGCs) in South Africa, Lesotho and Swaziland. At each grid cell, presence records for frog species were acquired based on either visual or audio evidence (Minter et al., 2004). Frogs, like birds, have distinctive calls that are unique to a species and this greatly enhances the ability to atlas frogs. Data collection was usually timed to correspond with the breeding season to optimise the discovery and identification of species based on breeding calls (Minter et al., 2004). Historical museum and archive data were included to augment the data collected during the atlas survey. Museums, personal databases and literature records were used as sources for historical data that covered approximately 100 years of sampling (Minter et al., 2004). Data were corrected for updated taxonomic classifications and doubtful records were excluded. Ultimately, 16 983 historical records were included to support the 25 486 records collected during the atlas period.

2.2.2. *Assessment of geographic sampling bias in SAFAP data*

Two different methodological approaches were used to analyse geographic sampling bias in the *SAFAP* data. The first approach used numbers of atlas records as an indication of the spatial variation in sampling intensity (Freitag et al., 1998; Parnell et al., 2003; Reddy & Dávalos, 2003). Relatively better-sampled areas were expected to have returned greater numbers of amphibian records. Thus, the collection density was computed and related to hypothesised sources of bias. The second approach employed species richness as a measure of sampling intensity. Higher sampling intensity in certain areas would have resulted in the detection of relatively more species. The number of species in each QDGC was used to identify gaps in sampling (Robertson & Barker, 2006).

2.2.3. *Biased collection density in relation to geographical features*

Collection density is the number of records per unit area (Freitag et al., 1998; Parnell et al., 2003). It is a reflection on both the abundance of amphibians and the sampling intensity in an area. For comparison with previous studies (Freitag et al., 1998; Parnell et al., 2003), we calculated the collection density 'per 100 km^2' for the entire study area. The number of records per QDGC mapped the spatial variation in collection density over the country.

The distribution of records was then spatially related to features hypothesised to allow ease of access to researchers and thus act as sources of sampling bias: cities, roads and protected areas. Observed numbers of records were computed as the number of records falling within certain distance categories from these features.

Cities: The six major cities in South Africa were used in this analysis: Bloemfontein, Cape Town, Durban, Johannesburg, Port Elizabeth, and Pretoria. These cities also house the institutions that contributed the most records to the *SAFAP*. Thus, distance from these cities was presumed to be the distance that herpetologists would have to travel to survey frogs.

Roads: The largest national roads were used, since these are the main routes that connect the major cities. QDGCs in the countries of Swaziland and Lesotho were excluded from this analysis due to lack of roads data. Roads are much smaller than the QDGCs through which they transect, and there are often many roads within a single QDGC. This meant that QDGCs could not easily be assigned to a certain distance from roads. So, roads data were converted into distance image maps (ArcGIS Spatial Analyst, “Distance”), such that each QDGC contained 25 smaller pixels. Each of these smaller pixels was assigned the distance to the nearest road (Parnell et al., 2003). Thus, the distances used are the average distance (km) to any national road within each QDGC.

Protected areas: Since there is a large variation in the size of protected areas, some QDGCs are completely enclosed within reserves, while other reserves are completely enclosed within a single QDGC. Thus, the zero distance class used in this analysis contained QDGCs that were either completely or mostly covered by protected areas. The 1 – 10 km distance class included cells that either partially intersected reserves or were located within 10 km of the reserve boundary. The QDGCs in the remaining distance classes had no direct contact with any reserve, but were located within the indicated distance from the protected area.

In line with several previous studies, expected number of records was calculated as “*Expected number of records = (Number of QDGCs within category/Total number of QDGCs) x Total number of records*”. Hence, the expected number of records became a function of the area covered by each distance category (Freitag et al., 1998; Parnell et al., 2003). Observed patterns in the distribution of records were compared to expected numbers and the differences indicated the level of sampling within a category (Freitag et al., 1998). Since observed and expected proportions were available per category, the appropriate statistical test was the chi-square test (McDonald, 2009). A separate chi-square test was performed for cities, roads and protected areas to test for a significant difference between the observed and expected patterns. Since the high sample size resulted in an unsuitably high power for these tests, a power analysis was conducted (Quinn & Keough, 2002; Lenth, 2006). A minimum effect size of 5% (or ≈ 2 000 records) was chosen as this was approximately the size of the sampling bias effect found in previous studies (Quinn & Keough, 2002; Parnell et al., 2003; Reddy & Dávalos, 2003). Thus, sample size of observed numbers of records was reduced proportionally for each test to obtain a power of 0.8 ($\beta = 0.2$, a conventional choice for power; Quinn & Keough, 2002; McDonald, 2009). We corrected for multiple tests using both the step-down Bonferroni and False Discovery Rate methods (McDonald, 2009). Only the corrected p-values are presented in the results section.

The location of cities, roads and protected areas are often correlated, since they are all manifestations of human presence (population density) within an area. Three correlations (cities vs. roads; cities vs. protected areas; roads vs. protected areas) were performed to test whether this covariance was evident at the QDGC resolution utilised here. Non-parametric (Spearman) correlations were used to account for possible non-normality in the measured distances from each feature (McDonald, 2009). These distances from features were the same categorical distances assigned to each QDGC and used in the previous analyses. Step-down Bonferroni and False Discovery Rate corrections for multiple tests were performed.

2.2.4. *Identifying sampling gaps based on species richness*

Species richness is defined as the number of species per unit area. The term species richness is usually used to describe real patterns of species location in space. However, when there is significant geographic sampling bias, measured species richness can be a function of the degree of sampling intensity (Dennis et al., 1999; Reddy & Dávalos, 2003; Ferreira et al., 2007). As sampling intensity increases, so measures of species richness become more dependent on the actual species richness and less dependent on the sampling intensity.

Funk and Richardson (2002) plotted the mean annual temperature and mean annual rainfall of all the QDGCs in their study area, thus creating a climate space in which they then plotted the rainfall and temperature variables of collecting sites. The gaps between collecting sites on the graph were then related back to a map of the study area to identify areas where conditions appear suitable, but which were not sampled. Robertson and Barker (2006) expanded on this method by using species richness values and adding heterogeneity variables to the analysis. The methods formulated by Robertson and Barker (2006) were followed here and are described below.

Mean annual rainfall and mean annual temperature were calculated for each QDGC from interpolated climate surfaces produced by the Climate Research Unit and based on weather station data (New et al., 2002). Each Quarter Degree Grid Cell was then plotted in a two-dimensional climate space defined by mean annual rainfall and mean annual temperature (Robertson & Barker, 2006). A bubble-plot was used to show how species richness varied within this climate space. The size of each bubble represented the number of species within each QDGC. The climate space was then divided into units of 100 mm rainfall by 2°C temperature. The QDGC with the highest species richness within each climate unit was then identified. QDGCs with less than 50% of this highest value were ‘possibly under-sampled’ (Robertson & Barker (2006) used the more conservative value of 20%). In addition, if these ‘possibly under-sampled’ cells had a greater topographic heterogeneity (standard deviation of altitude per QDGC; 900 pixels per QDGC) than the cell with the highest species richness, these were considered to be ‘probably under-sampled’ (Robertson & Barker, 2006). These categories were then mapped to illustrate which parts of South Africa were poorly sampled.

The proportions of well-sampled and under-sampled cells were then calculated for locations near to cities, roads and protected areas; and similarly for locations further from these features. The same distances that had significantly more amphibian records in the previous analysis were used as the threshold value for proximity to features. Results were presented as a stacked bar chart. Chi-square tests for independence were used to determine whether the proportion of ‘well-sampled’, ‘possibly under-sampled’ and ‘probably under-sampled’ QDGCs were the same at locations near to, or far from, geographic features (McDonald, 2009). Again, only the p-values after correction for multiple tests are given.

2.2.5. *Assessment of geographic sampling bias in the GAA species distribution data*

The IUCN commissioned the Global Amphibian Assessment to evaluate the status of all amphibians described worldwide. This analysis was completed in 2004 and updated during the 2008 IUCN Red List categorisation (IUCN, Conservation International & NatureServe, 2008). A product of this assessment was a set of geographic data that mapped the Extent of Occurrence of each amphibian species (IUCN, 2009). Extent of Occurrence is a measure of species distribution defined as the area within the shortest boundary drawn around all presence records of a species (IUCN, 2001). This measure reduces omission error, and geographic bias, in presence-only record data by encompassing poorly sampled areas within the boundary of known occurrences. It is therefore possible that GAA Extent of Occurrence data, while undoubtedly based on the *SAFAP* presence records, is a feasible bias-free alternative for use in conservation plans.

To test whether Extent of Occurrence measures reduce geographic bias, we obtained the GAA amphibian distribution data from the IUCN website (IUCN, 2009). The species distribution polygons were spatially joined to the South African QDGCs, and the species richness of each grid cell was calculated based on the number of species polygons it intersected. Since this provided species richness information, we then performed the same species richness analysis of sampling bias that was described above. The same climate units as before were used. Grid cells were classified into “well sampled”, “possibly under-sampled” or “probably under-sampled” and these categories were mapped.

2.3. Results

2.3.1. *Sources of geographic sampling bias in the SAFAP*

Collections from the entire dataset contributed an average collection density of 3.35 records per 100 km^2 (or 21 records per QDGC). However, the data were highly skewed, with many QDGCs containing low numbers of records (13.3% had no records) and few cells containing many records (742 specimens from a single cell in northern Swaziland). There was a clear gradient in number of records from the east to the west of the country with parts of the northeastern region and eastern coastline having the highest number of records per cell (>101) (Figure 1). The northwestern region and a few cells along the Drakensberg Mountains showed a paucity of records. The Cape coastline also contained many records, particularly in the surrounds of the city of Cape Town. Urban centres of Johannesburg, Pretoria, Bloemfontein and Durban also showed local increases in the number of records.

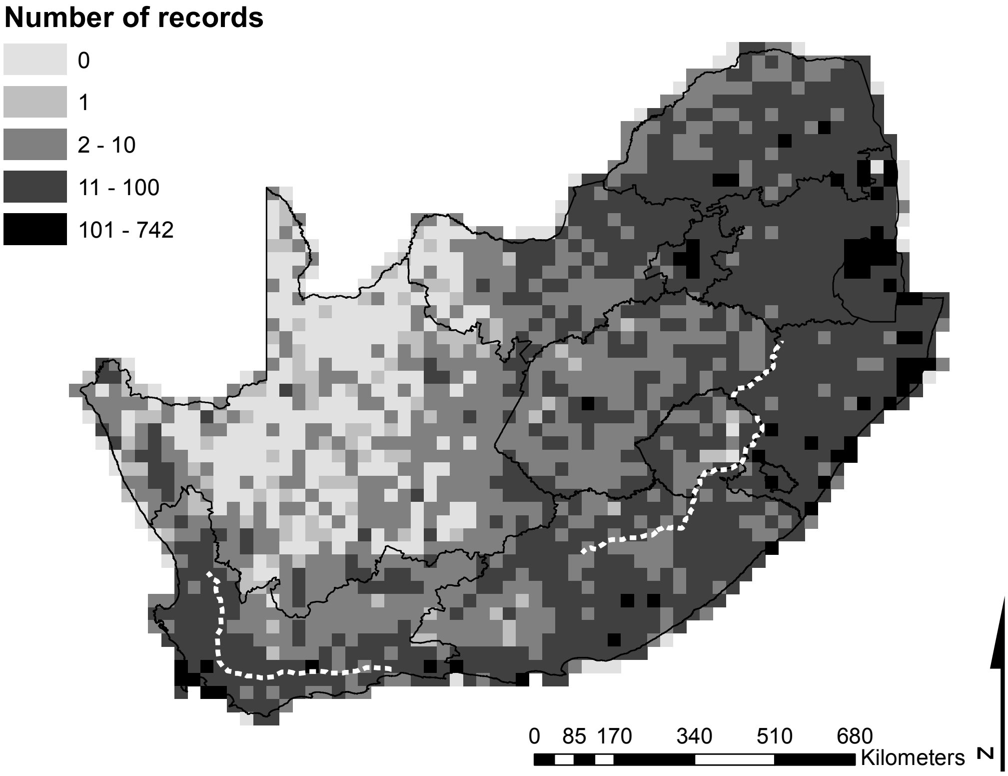


Figure 1: The spatial distribution of *South African Frog Atlas Project* records by Quarter Degree Grid Cell. The white dotted lines show the locations of the Cape Fold Mountains in the west and the Drakensberg Mountains in the east.

The results showed that the observed numbers of records were significantly different from expected in relation to cities ($\chi^2 = 91.871$; $p < 0.0001$), roads ($\chi^2 = 87.180$; $p < 0.0001$) and protected areas ($\chi^2 = 95.871$; $p < 0.0001$). There were substantially more records than expected within 100 km and even 200 km of cities (Figure 2a). Areas furthest from cities (more than 401 km) were poorly sampled, with 6 697 fewer records than expected. For national roads, there were 4 966 more records than expected within an average of 30 km from national roads (Figure 2b). Further than 30 km from a national road, there were fewer records than expected. Similar to cities and roads, the degree of sampling showed a decreasing trend with distance from protected areas (Figure 2c). QDGCs that fell entirely within, or less than 10 km from reserves were well sampled in comparison to other distance classes. The 1 – 10 km distance category was particularly well sampled, containing 10 482 more records than expected (Figure 2c). The areas further from reserves, in particular those further than 50 km, had many fewer records than were expected. Most cities, roads and protected areas were located in the eastern half of the country and along the southern coast (see inset maps in Figure 2). Spearman correlations confirmed the spatial associations between these features ($r = 0.21 – 0.40$, $p < 0.0001$). This reflects that fact that human population density and infrastructure development is higher in these areas.

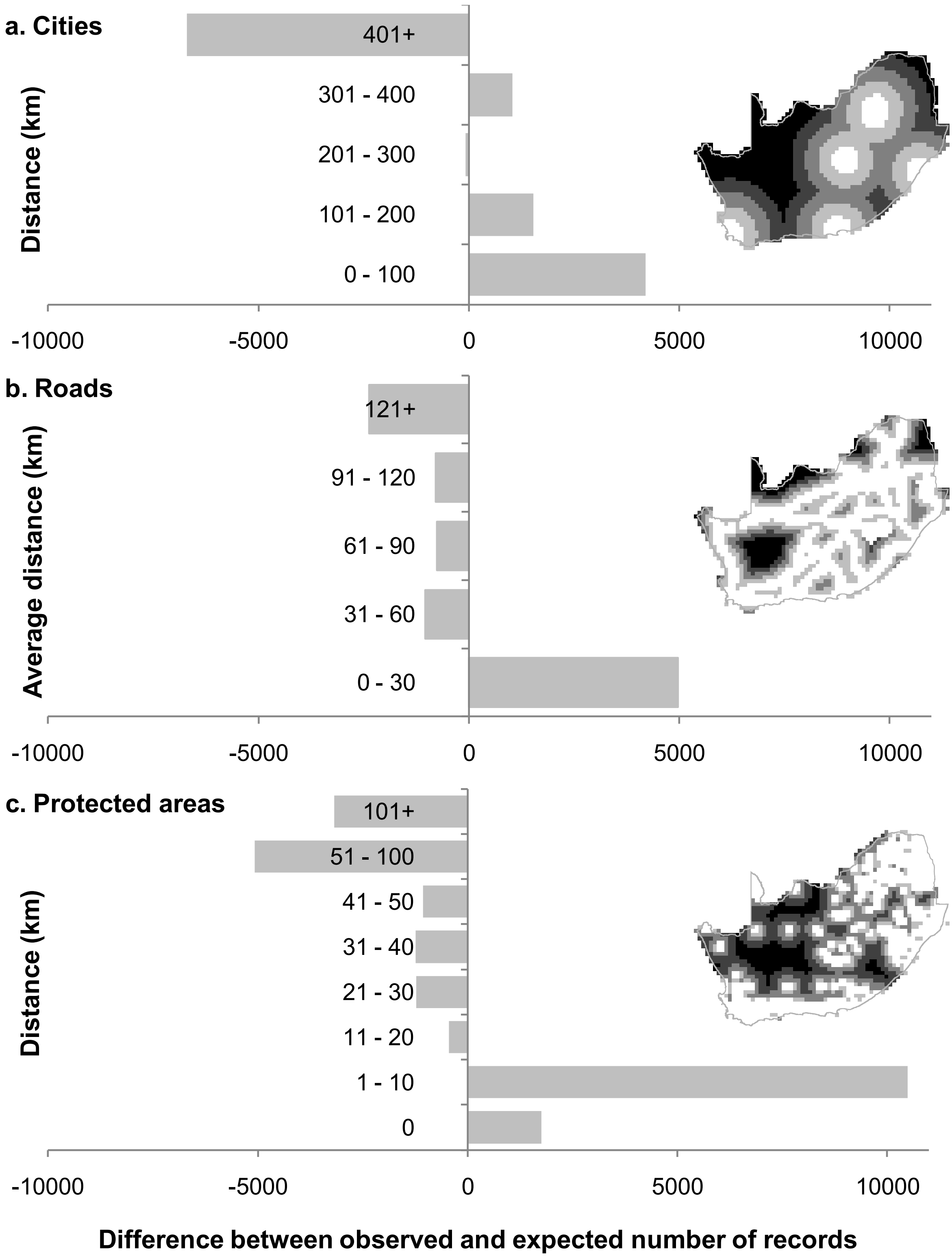


Figure 2: The difference between the observed number of records and expected number of records within certain distance categories from: (a.) cities, (b.) national roads and (c.) protected areas. The insets show maps of the same distance categories as the vertical axes, with progressively darker shades indicating increased distance from the features.

2.3.2. *Sampling gaps in the SAFAP based on species richness*

Species richness showed a similar east-west gradient as collection density, with many more species per grid cell on the eastern side of South Africa, and few species per cell in the north-west (Figure 3). The highest measure of species richness came from a grid cell on the northeastern coast, with a value of 49 species. The majority of the QDGCs in the country contained between two and ten species.

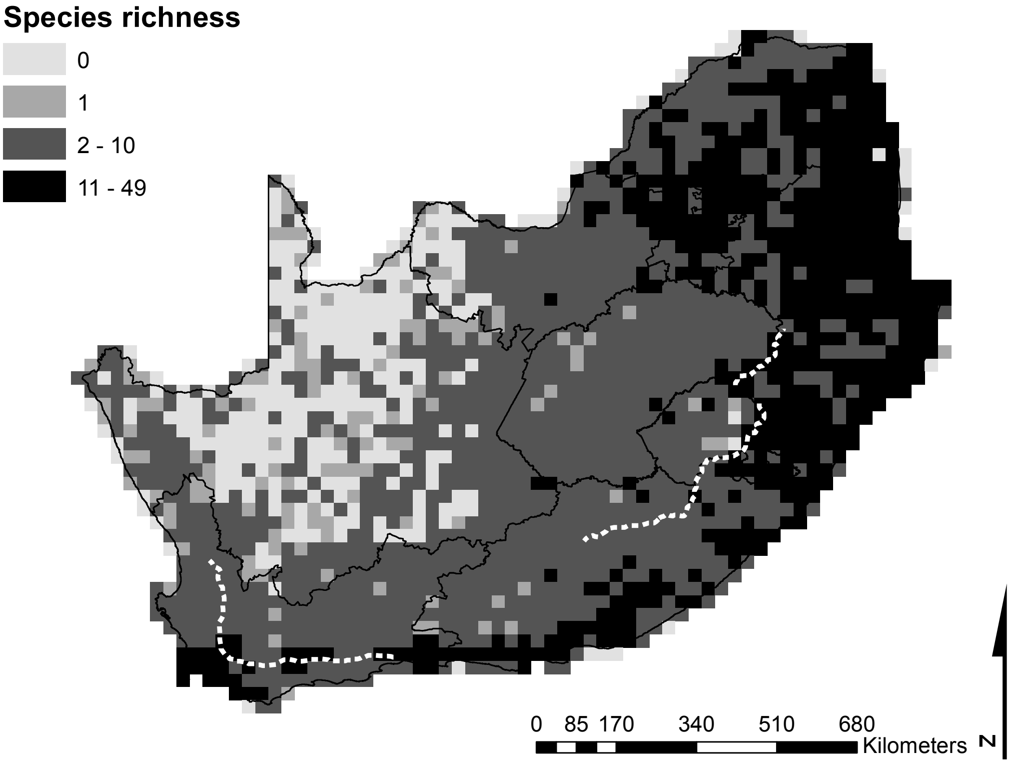


Figure 3: Measured species richness of amphibians per Quarter Degree Grid Cell. The white dotted lines show the locations of the Cape Fold Mountains in the west and the Drakensberg Mountains in the east.

When species richness was plotted within a two dimensional climate space, the highest species richness values were found with a combination of high temperature and high precipitation (Figure 4). QDGCs with lower than 400 mm mean annual precipitation had consistently lower measured species richness.

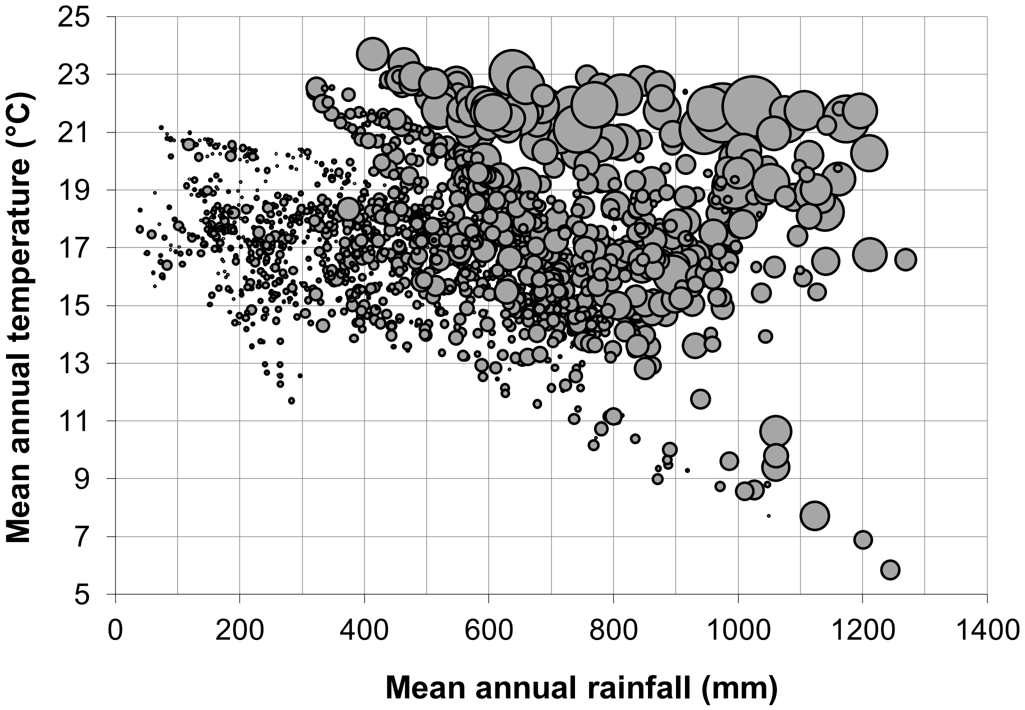


Figure 4: Each Quarter Degree Grid Cell is a point within a two-dimensional climate space defined by mean annual temperature and mean annual rainfall. The size of the bubble indicates the species richness of the QDGC, such that the larger the bubble the greater the numbers of species recorded in that grid cell. Climate variables are calculated from interpolated climate surfaces produced by the Climate Research Unit and based on weather station data (New et al., 2002).

The results of this climate and heterogeneity assessment of sampling bias showed that the eastern and coastal areas were better sampled than the central and western interior (Figure 5). Thirty-six percent of all QDGCs were well sampled. This analysis highlighted areas of high heterogeneity as the most likely to have been poorly sampled, in particular the cells which occur along the escarpment (Figure 5). “Probably under-sampled” grid cells made up 10% of the total number of QDGCs.

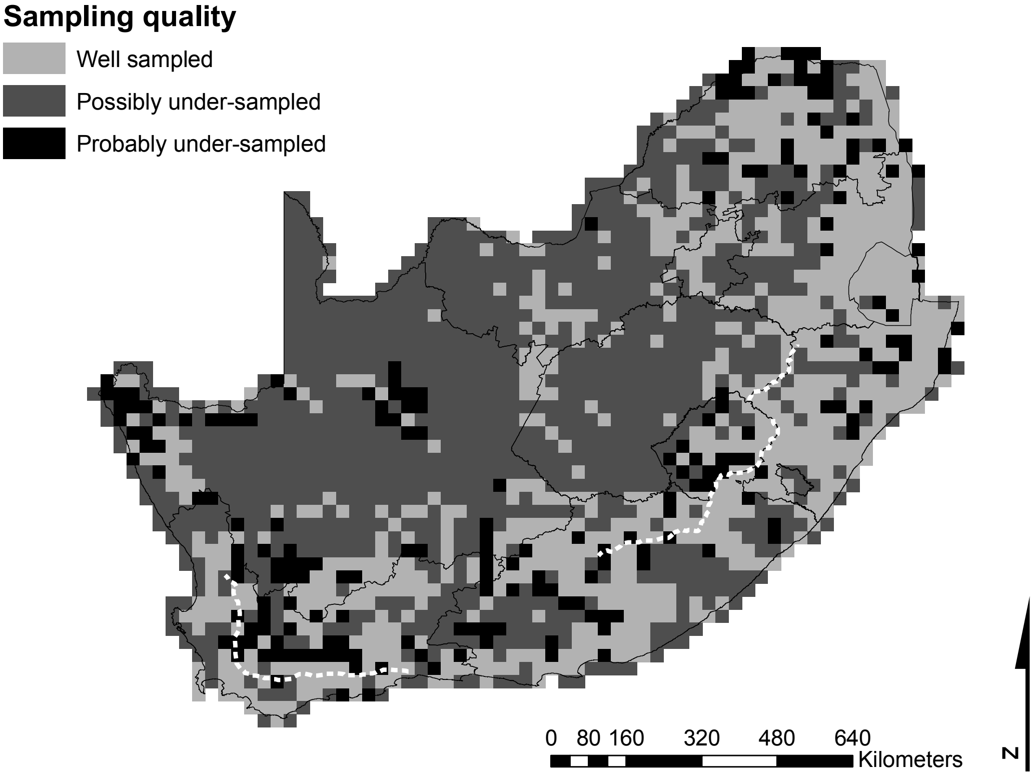


Figure 5: An assessment of the quality of sampling in the *SAFAP* database for each Quarter Degree Grid Cell, based on climate and heterogeneity. The pale grey cells have more than 50% of the highest species richness in their climate unit, and are considered to be well sampled. The darker grey cells have lower than 50% of the highest species richness in their climate unit, but also have lower heterogeneity. These cells are possibly under-sampled. The black QDGCs have lower than 50% of the highest species richness in their climate unit, but higher heterogeneity, and are probably under-sampled. The white dotted lines show the locations of the Cape Fold Mountains in the west and the Drakensberg Mountains in the east.

This species richness assessment again revealed significant differences in the quality of sampling regarding proximity to cities, roads and protected areas. Areas near to these features contained more well-sampled cells and fewer ‘probably under-sampled’ cells than areas further away. Within 200 km of cities, only 7.0% of QDGCs were ‘probably under-sampled’ (Figure 6), while further than 200 km from cities 11.6% of QDGCs fell into this category. This difference was significant according to a chi-square test ($\chi^2 = 10.742$; $p < 0.01$). Proximity to roads presented a similarly significant difference in sampling quality ($\chi^2 = 26.170$; $p < 0.0001$). In the vicinity of national roads, 41.5% of QDGCs were well sampled. This percentage decreased to 30.4 further than 30 km from roads. Again, protected areas showed the most pronounced difference ($\chi^2 = 170.447$; $p < 0.0001$). Only 25.5% of cells more than 10 km from protected areas were well sampled. Near to protected areas, this measure doubled, with 52.7% well sampled QDGCs within 10 km of protected areas.

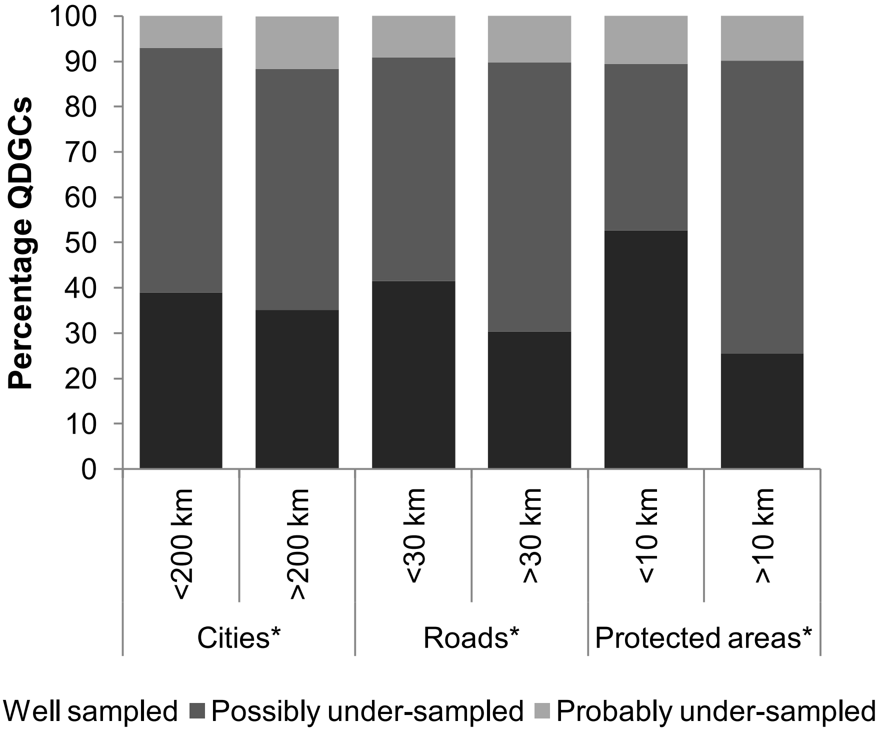


Figure 6: The percentage of well-sampled and under-sampled Quarter Degree Grid Cells within certain distances of cities, roads and protected areas. An asterisk (*) indicates a significant difference according to a chi-square test for independence (p < 0.05).

2.3.3. *Geographic bias in the GAA species distribution data*

The GAA polygons reduced much of the geographic sampling bias that was evident in the *SAFAP* presence data. The number of well-sampled grid cells increased to 86%, which covered the majority of the country including much of the arid western half (Figure 7). Only a small number of northern QDGCs remain ‘possibly under-sampled’. The numbers of ‘probably under-sampled’ QDGCs dropped to less than 2%, but these were still centred on the Cape Fold and Drakensberg Mountains.

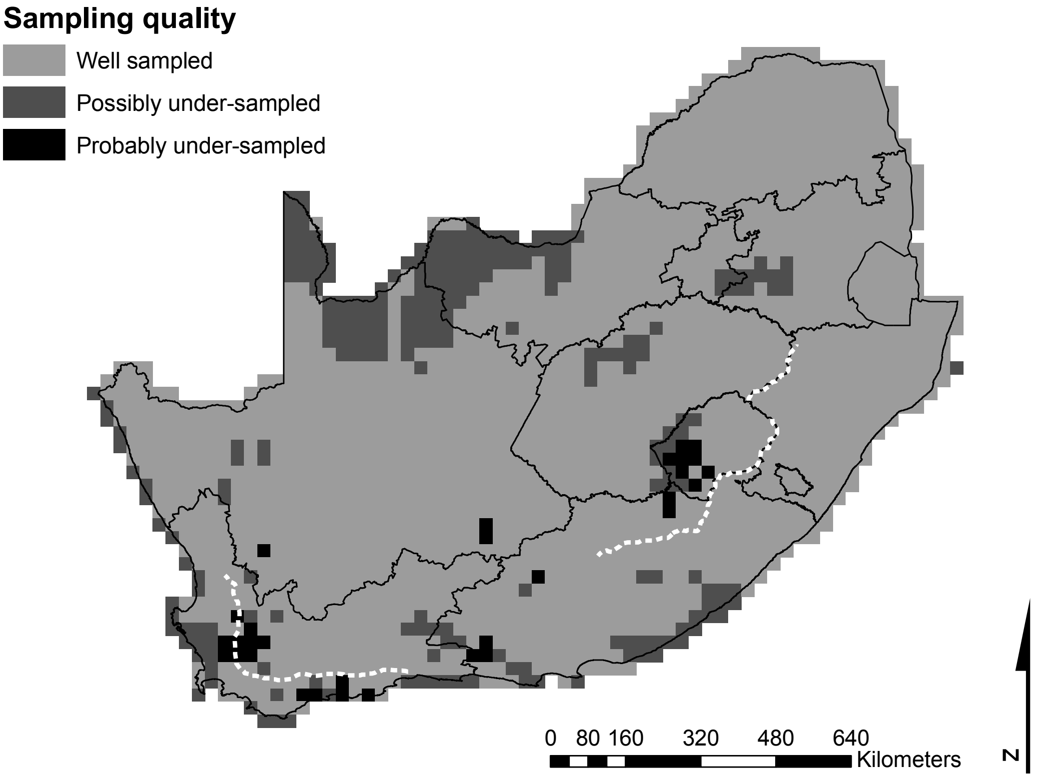


Figure 7: An assessment of the quality of sampling of GAA species distributions for each Quarter Degree Grid Cell, based on climate and heterogeneity. The pale grey cells have more than 50% of the highest species richness in their climate unit, and are considered to be well sampled. The darker grey cells have lower than 50% of the highest species richness in their climate unit, but also have lower heterogeneity. These cells are possibly under-sampled. The black QDGCs have lower than 50% of the highest species richness in their climate unit, but higher heterogeneity, and are probably under-sampled. The white dotted lines show the locations of the Cape Fold Mountains in the west and the Drakensberg Mountains in the east.

2.4. Discussion

The observed distribution of amphibian records in the *SAFAP* results from a combination of real biological pattern and geographic sampling bias. In deciding whether conservation planning can be reliably based on an atlas dataset, researchers must make a determination of which of these two processes has been foremost in producing the observed pattern (Funk et al., 1999). If variation in sampling intensity is exceedingly high, then sampling bias may completely obscure the real biological pattern. In this situation, use of the dataset for any form of conservation planning would be inappropriate. However, many authors believe that the general patterns of species richness and species range size can be reliably detected despite known geographical bias (Williams et al., 2002; Parnell et al., 2003). The acceptable level of geographic bias depends on many factors, including the objectives, scope, data formats and methodology employed within any particular conservation plan (Rouget et al., 2004; Rondinini et al., 2006; Robertson et al., 2010). This research provides both a quantitative and spatial assessment of geographic bias in the *SAFAP*, so that conservation planners can make an informed decision about whether the data are sufficiently complete to provide a reliable assessment.

In comparison to some other studies, the 3.35 amphibians recorded for every 100 km^2 represents relatively sparse sampling. Dunn and Weston (2008) conducted a review of bird atlases, and found that sampling intensity ranged from 2 – 8 480 records per 100 km^2 (with an average of 470 records per km^2). The first South African Bird Atlas amassed 7 million records of avian occurrence, a collection density of over 550 records per 100 km^2 (Harrison et al., 2008). This was due to the participation of over 5 000 members of the public, who added substantially to the database (Harrison et al., 2008). In contrast, only 420 volunteers submitted amphibian records to the *SAFAP*, and the majority of the records came from experienced herpetologists (Minter et al., 2004). This reflects not only the lower level of public interest in amphibians, but also some of the difficulties involved in frog atlasing: amphibians are nocturnal, they are generally restricted to water sources, are often only seasonally active and cryptic species require expert knowledge to identify with certainty. However, conservation plans that only include well-sampled 'indicator' taxa are not representative of all aspects of biodiversity (Larsen et al., 2009a). The *SAFAP* is currently the most comprehensive dataset for amphibians in South Africa (Minter et al., 2004). It presents the only opportunity for this often-overlooked taxon to be included in conservation plans.

Collection density of the *SAFAP* records varied widely over the country. This variation followed a predictable pattern with a clear east-to-west gradient in collection density. The eastern parts of the country and the southern coastline had many more occurrence records than the arid central western interior. There was also a significant association between the location of amphibian records and human infrastructure. Cities, roads and protected areas are most commonly located within the eastern part of the country, where human population density is highest (Chown et al., 2003; Evans et al., 2006). The association between these features and a high collection density may be only a consequence of spatial congruence between amphibian distribution patterns and human activities. Evans et al. (2006) found that human population density in South Africa was well correlated with both bird and amphibian richness along this east-to-west gradient. Neither human populations nor amphibian species diversity were concentrated in desert areas. This relationship between species richness and human population density is also evident for other vertebrate taxa in Africa and is primarily attributed to similar use of environmental energy (Reddy & Dávalos, 2003, Chown et al., 2003; Evans et al., 2006). Temperature, precipitation and net primary productivity all follow an analogous variation from high values in the eastern part of South Africa to lower values in the west (Chown et al., 2003; Evans et al., 2006). This finding complicates the separation between sampling bias and real biological pattern that is necessary to assess the worth of atlas data for conservation planning. Evans et al. (2006) conclude that bias in sampling effort plays only a minor part, if any, in this correlation. Conversely, Reddy & Dávalos (2003) suggest that sampling bias may actually be responsible for the correlation due to high sampling in populated areas.

A species richness approach, which accounted for climatic variables and topographical heterogeneity, provided an alternative measure of sampling quality to facilitate the resolution of this issue. Only cells with similar climatic conditions were compared and then those with lower topographic heterogeneity were held to a lower standard of expected species richness. A possible limitation of this method is that the choice of a threshold for poorly sampled areas is arbitrary. Robertson and Barker (2006) used a threshold of 20% of the value in the most species rich cell. Increasing the threshold value to 50% meant that our assessment of sampling quality was more rigorous and more cells were considered under-sampled. There was a distinct relationship between the climate in a QDGC and its amphibian species richness. Had this not been the case, the use of this method would have been uninformative. High species richness was associated with a combination of high mean annual rainfall and high mean annual temperature. Cells with low rainfall (below 400 mm) all had low species richness values. Robertson and Barker (2006) found a similar relationship with rainfall when assessing species richness maps from the National Herbarium’s plant database for southern Africa.

This method reiterates the fact that large parts of the central western interior were under-sampled. This result is comparable to that of Robertson and Barker (2006) who found that plants were also under-sampled in this region. Similarities in the locations of under-sampled areas between amphibians and plants suggest that factors determining geographic sampling bias may be consistent across taxa. ‘Probably under-sampled’ were many topographically heterogeneous cells along the Cape Fold Mountains and Drakensberg escarpment. The same areas of incomplete coverage acknowledged by the editors of the *SAFAP* are highlighted here, namely arid and montane regions (Minter et al., 2004). Moreover, the specific grid cells in which this under-sampling manifested were pinpointed.

Relating this species richness measure of sampling quality to cities, roads and protected areas confirmed that the higher numbers of amphibian records in close proximity to these features were the result of significantly more well sampled cells. Herpetologists involved in surveying frogs concentrated their efforts within a 100 km radius of their residences and places of work in the major cities: the syndrome of the easy day trip. When travelling further afield, they followed the major national roads and sampled preferably within 30 km of these convenient routes. In addition to bias towards easily accessed areas, our results indicate that researchers do focus on areas that they believe to have a higher biodiversity. There were significantly more well sampled QDGCs within 10 km of protected areas. Researchers likely target these areas due to their natural state and perceived higher biodiversity. Roads and protected areas may also provide sampling opportunities in publically accessible areas. This minimises potentially time consuming and complex negotiations with multiple private landowners. Thus, despite the attempt at systematic sampling on the part of the atlas researchers, cities, roads and protected areas received a disproportionate amount of sampling effort.

We have shown that the data in the *SAFAP* contains significant geographical bias and substantial sampling gaps, but is this bias extensive enough to mask the real pattern of biodiversity? There is some evidence that suggests that the observed patterns represent true amphibian species richness and abundance in South Africa. The broad scale east-to-west gradient is prominent in both the numbers of records and species richness. This gradient follows a real moisture gradient across the country and species richness was consistently low in low rainfall regions. Amphibian reproduction is highly dependent on the availability of standing water and the pattern of rainfall (McCarty, 2001; Carey & Alexander, 2003) and thus this relationship is theoretically valid. The observed species richness patterns are also consistent with biogeographical theories concerning the relative distributions of tropical and temperate species (see Alexander et al., 2004). Furthermore, this broad east-to-west gradient is not unique to amphibians. Species richness of birds recorded from the *South African Bird Atlas Project* (Fairbanks et al., 2002) and plants from the National Herbarium's plant database (PRECIS; Robertson & Barker, 2006) showed a similar gradient. In the *SAFAP*, it is likely that both the real pattern in biodiversity and the pattern of sampling bias both follow an east-to-west gradient. Thus, the east-to-west gradient in amphibian richness is a real pattern, but it may well have been exaggerated by sampling bias. While the broadest scale patterns are generally discernable from the *SAFAP*, significant levels of geographic sampling bias mean that the dataset may not be sufficiently accurate at the finer scales optimal for systematic conservation planning (Rouget et al., 2004).

The GAA species distribution data generalised the pattern of amphibian species richness in South Africa, decreasing local heterogeneity in the number of species recorded. This reduced, but did not altogether eliminate, the geographic bias that was evident within the *SAFAP*. The same arid and mountainous regions still displayed some geographic bias. Whilst minimising much of the concern with bias associated data, these simplified species boundaries do not necessarily provide a superior alternative to biological atlases. The global nature of the GAA data means that they provide little more than the broad-scale amphibian distribution patterns already apparent within the *SAFAP* data. Despite decreased omission error, the data are now subject to increased commission error: the incorrect assumption of species presence (Rondinini et al., 2006). Commission error renders most alternative datasets ineffective for conservation planning at a scale suitable for implementation. Accurate, up-to-date and formally documented species occurrence data is generally a better option for including species distributions into fine scale conservation planning. Until a dataset is available that minimises both omission and commission error, conservationists must consider the implications of including flawed data in their plans.

Any biodiversity-based conservation planning requires the comparison of biodiversity between regions. In datasets that contain significant geographic sampling bias, these kinds of comparisons are ill-advised, since species richness can be both under- and overestimated relative to regions with differing sampling intensity (Williams et al., 2002; Reddy & Dávalos, 2003; Boakes et al., 2010; Robertson et al., 2010). Overestimated biodiversity may seem an unlikely difficulty, since the better sampled an area, the closer the measured species richness is to the true value. However, when certain areas are preferentially sampled, the species richness appears elevated in relation to poorly sampled areas. Conservation plans will consequently afford greater priority to those areas for which sampling was more intense, rather than areas with real high biodiversity. If the distributions of important species are included in the conservation plans, geographic sampling bias will have a similar effect. These species will have had a higher probability of detection, and more presence records, in well-sampled grid cells and will therefore impart higher irreplaceability to these areas.

The association between high sampling intensity and human infrastructure is likely to increase conservation conflicts around metropolitan areas. Conservation conflicts occur when high biodiversity coincides spatially with high human activity, and land-use planners must make difficult decisions between conservation and development (Chown et al., 2003; Van Rensburg et al., 2004). Conservation conflicts may be unavoidable when species richness correlates with high human population density, as is the case in South Africa (Chown et al., 2003; Van Rensburg et al., 2004; Evans et al., 2006). However, it would be unfortunate if these problems were amplified by sampling bias. Geographic sampling bias towards cities and roads in the *SAFAP* means that the perception of species richness near to these features is inflated relative to other areas. The cells surrounding cities and roads will contain an apparently high number of species occurrences within a smaller area, increasing their value in complementary selection algorithms. Areas near to human infrastructure are generally highly transformed and priority for reserve selection in these areas should be avoided rather than enhanced.

The symptoms of this bias are evident in the irreplaceability map for endemic and threatened animals in the National Spatial Biodiversity Assessment. Seven datasets, including the *SAFAP*, formed the basis for this map (Rouget et al., 2004). Grid cells in the province with the highest human population density, Gauteng, showed high irreplaceability scores in this assessment. Other populous cities: Cape Town, Durban and Port Elizabeth also had high irreplaceability. This bias is also carried through to regional biodiversity assessments, such as the Gauteng State of the Environment Report, which asserts that the province "represents a relatively large proportion of South Africa's biodiversity in a small area" (GDACE, 2004). In Gauteng and other provinces with high population density, the priority for conservation may be exaggerated due to high sampling intensity and this may be incompatible with essential social development.

Another important part of systematic conservation planning is the assessment of the current reserve system. This gap-analysis stage identifies how well current reserves meet the conservation targets (Margules & Pressey, 2000). Historically, issues of biodiversity conservation received little attention during the placement of South African reserves. The current protected area system is thus an inadequate representation of biodiversity (Driver et al., 2005). However, if a biased dataset is used in the evaluation of current reserves, they may appear to conserve either high species richness or a high percentage of an individual species distribution.

In the *SAFAP* database, there were considerably more amphibian records and double the number of well-sampled QDGCs within 10 km of protected areas. This result was similar to that of Reddy and Dávalos (2003) who found that bird species were much better sampled within and surrounding the protected areas of sub-Saharan Africa. Since conservation of frog species is rarely the primary justification for the establishment of protected areas and amphibians are not restricted to reserves, this situation signifies a legitimate and substantive sampling bias. This bias will negatively affect evaluations of the effectiveness of the current reserve network for the conservation of amphibians. Current reserves will apparently contribute highly to amphibian biodiversity targets, when in reality these areas have just been preferentially sampled in comparison to other regions. Using the GAA alternative data will yield a similar problem. Commission error may mean that many species appear to be protected when in reality there are few actual occurrences within the current reserve system (Rondinini et al., 2006). Furthermore, this may result in future conservation plans assigning priority to areas in which the important biodiversity features do not occur (Rondinini et al., 2006).

Overestimated species richness may falsely enhance the conservation priority of certain areas, or make protected areas seem particularly effective. Underestimated species richness is an equally severe problem. It causes conservation plans to neglect areas that should have received high priority (Reddy & Dávalos, 2003). Sampling of amphibians was poor in remote areas, which consequently had low measured species richness. In the *SAFAP*, large parts of the arid west had poor sampling intensity. These areas represent almost the entirety of the Succulent Karoo, Nama-Karoo and Desert biomes. While it is unlikely that these arid areas would ever achieve the high species richness of the tropical eastern parts of the country, additional records will possibly result in the discovery of further species occurrences. Thus, these areas may have an important contribution to make to biodiversity conservation in the country, but at present, they will be overlooked during the conservation planning process. Exchanging *SAFAP* presence records for species distribution polygons in poorly sampled areas would enhance the inclusion of these areas into conservation plans. However, when few occurrence data are available (as is the case for arid specialist amphibians in South Africa), the construction of species distributions becomes more speculative and less precise (Rondinini et al., 2006), with obvious implications for the accuracy of conservation plans.

Gaston and Rodrigues (2003) tested the effects of different data types on reserve selection, and found that even presence-absence datasets with low sampling effort can be effective in producing reasonable reserve networks. However, the scenario that they applied maintained equal sampling for every grid cell i.e. no geographic bias. Thus, if the geographic bias in the *SAFAP* could be minimised without concurrent increase in commission error, the dataset could become invaluable to conservation planning. To achieve this, sampling should be intensified in areas and for taxa known to have poor sampling effort in the past (Parnell et al., 2003; Reddy & Dávalos, 2003; Küper et al., 2006). The *SAFAP* itself has been helpful in identifying the areas that require additional sampling (Donald & Fuller, 1998; Dennis & Shreeve, 2003; Graham et al., 2004). Dennis and Shreeve (2003) found that focused sampling as part of a new atlas of French butterflies addressed extensive under-sampling in previous atlases.

The geographic bias within the *SAFAP* could be minimised by additional targeted sampling. The arid northwestern region of the country held few well-sampled QDGCs and many grid cells with no amphibian records. This entire region would benefit from additional sampling. The distributions of common and widespread species undoubtedly extend further into this region than is currently documented (Minter et al., 2004). More records of little known arid specialists would improve knowledge of their distributions and life histories. Precipitation is scarce and unpredictable in this region. In these situations, amphibians are generally fossorial and breed opportunistically, awaiting good conditions before emerging (Skelly et al., 2003). It may take many sampling trips, specifically timed to brief periods of amphibian activity, before the bias in this region is completely reversed. Conversely, the under-sampled QDGCs in topographically heterogeneous mountainous areas require only that researchers overcome the logistical travel difficulties. These areas should then return additional records and species occurrences within a short timeframe. The Cape Fold Mountains, Lesotho Highlands, Limpopo Highlands and some QDGCs along the Eastern Escarpment should be the target of supplementary sampling.

It is unlikely that any projects harnessing 'citizen science' could be completely free from geographic sampling bias. Volunteers are increasingly vital contributors to broad-scale atlas datasets (Boakes et al., 2010), but systematic and standardised sampling cannot be demanded of them (Robertson et al., 2010). Since standardised surveys are seldom achievable, it is imperative that sampling effort is precisely recorded. Person-hours, the number of visits to an area, the distance travelled whilst observing, search methods or some combination of similar survey effort variables must be documented (Dennis et al., 1999; Gaston & Rodrigues, 2003; Romo et al., 2006; Robertson et al., 2010). The second *South African Bird Atlas Project* attempts to achieve this by requiring a strict sampling protocol per datasheet submitted. A single datasheet provides for a maximum five-day sampling period in a particular pentad. Sampling must begin with an initial continuous two hours of observation, and hourly observations thereafter must be noted (www.sabap2.adu.org.za). Thus, a temporal unit of sampling has been created (Robertson et al., 2010). Furthermore, technological advances have increased the options for communication between project administrators and volunteers. Improved information dissemination means that participants can be notified of locations requiring additional sampling whilst the project is ongoing (Robertson et al., 2010). Again, the South African Bird Atlas 2 website provides a monthly updated gap analysis map and reports on the achievement of the project goals (www.sabap2.adu.org.za).

Improved surveys will no doubt amass far superior data in terms of coverage, comprehensiveness and quality. However, there is urgency in the requirement for data with which to analyse the anthropogenic effects on species ranges and for the prioritisation of conservation. Concern for certain taxa, especially amphibians, means that investigations aimed at identifying threats and creating conservation plans must proceed without unnecessary delay (Skelly et al., 2003; Tyre et al., 2003).

In the interim, the *SAFAP* presents the best available dataset of amphibian occurrence in South Africa. Conservation planners will have to employ methods that reduce the effects of geographic sampling bias. While using GAA species distributions presents an easily available opportunity to reduce geographic bias, the global scale of these data means that uncertainties arising from commission error are maximised. We have provided a simple score of sampling quality in the *SAFAP* based on climate and heterogeneity for each QDGC. This could be used to weight analyses in a manner similar to initiatives that have measured recorder effort (Elphick, 1997). Other options include bioclimatic modelling, which can fill gaps in sampling and enhance incomplete datasets. Modelling predicts the probability of occurrence of species based on environmental relationships discovered from the primary data (Dennis & Shreeve, 2003; Reddy & Dávalos, 2003; Graham et al., 2004; Segurado & Araújo, 2004; Küper et al., 2006). Prior to this assessment of sampling bias, there were only vaguely stated concerns about the standard of *SAFAP* occurrence data and its potential biases. The applicability of the *SAFAP* as the primary data for niche modelling was indeterminate. It would now be possible to state the sampling quality of QDGCs included in particular species models, and hence give an assessment of model quality. Some conservation planners choose only to include adequately sampled species and regions. For this reason, only Threatened and endemic amphibians were included in the National Spatial Biodiversity Assessment (Rouget et al., 2004). In areas with poor biodiversity data, expert knowledge can be used to define areas of high biodiversity (Berliner & Desmet, 2007). All of these measures rely to a greater or lesser extent on the original survey data and geographic bias will influence their accuracy. We therefore recommend that a detailed description of geographic bias accompany any use of an atlas dataset. In addition, preliminary conservation plans constructed using biased data must be re-evaluated once improved data becomes available.

2.5. References

Alexander, G. J., Harrison, J. A., Fairbanks, D. H. & Navarro, R. A. (2004) Biogeography of the Frogs of South Africa, Lesotho and Swaziland. In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H.H., Bishop, P. J. & Kloepfer, D. (eds) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

Berliner, D. & Desmet, P. (2007) Eastern Cape Biodiversity Conservation Plan: Technical Report. Department of Water Affairs and Forestry Project No 2005-012, Pretoria.

Boakes, E. H., McGowan, P. J. K., Fuller, R. J., Chang-qing, D., Clark, N. E., O'Connor, K. & Mace, G. M. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8: e1000385.

Carey, C. & Alexander, M. A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9: 111-121.

Chown, S. L., Van Rensburg, B. J., Gaston, K. J., Rodrigues, A. S. L. & Van Jaarsveld, A. S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* 13: 1233-1241.

Dennis, R. L. H. & Shreeve, T. G. (2003) Gains and losses of French butterflies: tests of predictions, under-recording and regional extinction from data in a new atlas. *Biological Conservation* 110: 131-139.

Dennis, R. L. H., Sparks, T. H. & Hardy, P. B. (1999) Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Desmet, P. & Cowling, R. (2004) Using the species-area relationship to set baseline targets for conservation. *Ecology and Society* 9: (online) http://www.ecologyandsociety.org/vol9/iss2/art11. Cited 30 July 2010

Desmet, P., Schaller, R. & Skowno, A. (2008) North West Province Conservation Assessment Technical Report. North West Province Department of Agriculture, Conservation & Environment, Mafikeng.

Donald, P. F. & Fuller, R. J. (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study* 45: 129-145.

Driver, A., Maze, K., Rouget, M., Lombard, A. T., Nel, J., Turpie, J. K., Cowling, R. M., Desmet, P., Goodman, P., Harris, J., Jonas, Z., Reyers, B., Sink, K. & Strauss, T. (2005) National Spatial Biodiversity Assessment 2004: priorities for biodiversity conservation in South Africa. *Strelitzia* 17. South African National Biodiversity Institute, Pretoria.

Dunn, A. M. & Weston, M. A. (2008) A review of terrestrial bird atlases of the world and their application. *Emu* 180: 42-67.

Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Fishpool, L. D. C., Foster, M., Knox, D., Langhammer, P., Matiku, P., Radford, E., Salaman, P., Sechrest, W., Smith, M. L., Spector, S. & Tordoff, A. (2004) Key Biodiversity Areas as Site Conservation Targets. *BioScience* 54: 1110-1118.

Elphick, C. S. (1997) Correcting avian richness estimates for unequal sample effort in atlas studies. *Ibis* 139: 189-190.

Evans, K. L., Van Rensburg, B. J., Gaston, K. J. & Chown, S. L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography* 15: 625-636.

Fairbanks, D. H. K., Kshatriya, M., Van Jaarsveld, A. S. & Underhill, L. G. (2002) Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* 5: 61-73.

Ferrar, A. A. & Lötter, M. C. (2007) Mpumalanga Biodiversity Conservation Plan Handbook. Mpumalanga Tourism and Parks Agency, Nelspruit.

Ferreira, D., Malard, F., Dole-Olivier, M.-J. & Gilbert, J. (2007) Obligate groundwater fauna of France: diversity patterns and conservation implications. *Biodiversity and Conservation* 16: 567-596.

Ferrier, S. (2002) Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here? *Systematic Biology* 51: 331-363.

Ferrier, S., Powell, G. V. N., Richardson, K. S., Manion, G., Overton, J. M., Allnutt, T. F., Cameron, S. E., Mantle, K., Burgess, N. D., Faith, D. P., Lamoreux, J. F., Kier, G., Hijmans, R. J., Funk, V. A., Cassis, G. A., Fisher, B. L., Flemons, P., Lees, D., Lovett, J. C. & Van Rompaey, R. S. A. R. (2004) Mapping More of Terrestrial Biodiversity for Global Conservation Assessment. *BioScience* 54: 1101-1109.

Freitag, S., Hobson, C., Biggs, H. C. & Van Jaarsveld, A. S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Animal Conservation* 1: 119-127.

Funk, V. A., Zermoglio, M. F. & Nasir, N. (1999) Testing the use of specimen collection data and GIS in biodiversity exploration and conservation decision making in Guyana. *Biodiversity and Conservation* 8: 727-751.

Funk, V. A. & Richardson, K. S. (2002) Systematic Data in Biodiversity Studies: Use It or Lose It. *Systematic Biology* 51: 303-316.

Gaston, K. J. & Rodrigues, A. S. L. (2003) Reserve Selection in Regions with Poor Biological Data. *Conservation Biology* 17: 188-195.

GDACE. (2004) Chapter 8: Biodiversity. In: Gauteng Conservation State of the Environment Report, Gauteng Department of Agriculture, Conservation and the Environment, Gauteng Provincial Government.

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C. & Townsend Peterson, A. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19: 497-503.

Harrison, J. A., Minter, L. G. & Burger, M. (2004) Atlas and Red Data book for frogs completed. *South African Journal of Science* 100: 11-13.

Harrison, J. A., Underhill, L. G. & Barnard, P. (2008) The seminal legacy of the Southern African Bird Atlas Project. *South African Journal of Science* 104: 82-84.

IUCN (2001) Categories & Criteria (version 3.1). Prepared by the IUCN Species Survival Commission. IUCN, Gland. http://www.iucnredlist.org/static/categories_criteria_3_1. Cited 16 July 2010.

IUCN (2009) IUCN Red List of Threatened Species. Version 2009.1. http://www.iucnredlist.org. Cited 15 June 2009.

IUCN, Conservation International and NatureServe (2008) 2008 IUCN Red List www.iucnredlist.org/amphibians. Cited 18 October 2010.

Küper, W., Sommer, J. H., Lovett, J. C. & Barthlott, W. (2006) Deficiency in African plant distribution data – missing pieces of the puzzle. *Botanical Journal of the Linnean Society* 150: 355-368.

Larsen, F. W., Bladt, J. & Rahbek, C. (2009a) Indicator taxa revisited: useful for conservation planning? *Diversity and Distributions* 15: 70-79.

Larsen, R., Holmern, T., Prager, S. D., Maliti, H. & Røskaft, E. (2009b) Using the extended quarter degree grid cell system to unify mapping and sharing of biodiversity data. *African Journal of Ecology* 47: 382-392.

Lenth, R. V. (2006) Java applets for power and sample size [Computer software]. http://www.stat.uiowa.edu/*rlenth/Power. Cited 26 February 2009.

Margules, C. R. & Pressey, R. (2000) Systematic conservation planning. *Nature* 405: 243-253.

McCarty, J. P. (2001) Ecological Consequences of Recent Climate Change. *Conservation Biology* 15: 320-331.

McCollin, D., Moore, L. & Sparks, T. H. (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation* 92: 249-263.

McDonald, J. H. (2009) *Handbook of Biological Statistics*, 2nd edn. Sparky House Publishing, Baltimore, Maryland.

Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H., Bishop, P. J. & Kloepfer, D. (eds) (2004) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research* 21: 1-25

Parnell, J. A. N., Simpson, D. A., Moat, J., Kirkup, D. W., Chantaranothai, P., Boyce, P. C., Bygrave, P., Dransfield, S., Jebb, M. H. P., Macklin, J., Meade, C., Middleton, D. J., Muasya, A. M., Prajaksood, A., Pendry, C. A., Pooma, R., Suddee, S. & Wilkin, P. (2003) Plant collecting spread and densities: their potential impact on biogeographical studies in Thailand. *Journal of Biogeography* 30: 193-209.

Pressey, R. (2004) Conservation Planning and Biodiversity: Assembling the Best Data for the Job. *Conservation Biology* 18: 1677-1681.

Quinn, G. P. & Keough, M. J. (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography* 30: 1719-1727.

Robertson, M. P. & Barker, N. P. (2006) A technique for evaluating species richness maps generated from collections data. *South African Journal of Science* 102: 77-84.

Robertson, M. P., Cumming, G. S. & Erasmus, B. F. N. (2010) Getting the most out of atlas data. *Diversity and Distributions* 16: 363-375.

Romo, H., García-Barros, E. & Lobo, J. M. (2006) Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29: 873-885.

Rondinini, C., Wilson, K. A., Biotani, L., Grantham, H. & Possingham, H. P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136-1145.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R. M., Mucina, L. & Rutherford, M. C. (2004) South African National Spatial Biodiversity Assessment 2004: Technical Report. Volume 1: Terrestrial Component. South African National Biodiversity Institute, Pretoria.

Segurado, P. & Araújo, M. B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31: 1555-1568.

Skelly, D. K., Yurewics, K. L., Werner, E. E. & Relyea, R. A. (2003) Estimating Decline and Distributional Change in Amphibians. *Conservation Biology* 17: 744-751.

South African Bird Atlas 2 website. http://sabap2.adu.org.za. Cited 30 July 2010

Telfer, M. G., Preston, C. D. & Rothery, P. (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation* 107: 99-109.

Turner, A. A. & De Villiers, A. L. (2007) Chapter 4: amphibians. In: Western Cape State of Biodiversity Report 2007. Scientific Services, CapeNature.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K. & Possingham, H. P. (2003) Improving Precision and Reducing Bias in Biological Surveys: Estimating False-Negative Error Rates. *Ecological Applications* 13: 1790-1801.

Van Jaarsveld, A. S., Freitag, S., Chown, S. L., Muller, C., Koch, S., Hull, H., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M. W. & Scholtz, C. H. (1998a) Biodiversity Assessment and Conservation Strategies. *Science* 279: 2106-2108.

Van Jaarsveld, A. S., Gaston, K. J., Chown, S. L. & Freitag, S. (1998b) Throwing biodiversity out with the binary data? *South African Journal of Science* 94: 210.

Van Rensburg, B. J., Erasmus, B. F. N., Van Jaarsveld, A. S., Gaston, K. J. & Chown, S. L. (2004) Conservation during times of change: correlations between birds, climate and people in South Africa. *South African Journal of Science* 100: 266-272.

Williams, P. H., Margules, C. R. & Hilbert, D. W. (2002) Data requirements and data sources for biodiversity priority area selection. *Journal of Bioscience* 27: 327-338.

Chapter 3: Range change methods

Botts, E. A., Erasmus, B. F. N. and Alexander, G. J. (2012) Methods to detect species range size change from biological atlas data: A comparison using the *South African Frog Atlas Project*. *Biological Conservation* 146: 72-80, http://www.sciencedirect.com/science/article/pii/S0006320711004514

3.1. Introduction

In a world of increasing extinction rates and rising anthropogenic pressure on ecosystems, species declines are not only a prediction for the future but also a contemporary trend. Amphibian declines were first observed in 1989, and continue to be a significant component of species loss occurring worldwide (Phillips, 1990; Stuart et al., 2004). Documenting species that have already declined is an urgent task (Tingly & Beissinger, 2009). Species with documented declines can receive priority conservation action through IUCN classification (IUCN, 2001) or other species-specific initiatives. Generalisations can provide comparative information on either taxa or regions most at risk, and the attributes that make them so (Kotze & O'Hara, 2003; Eken et al., 2004; Sodhi et al., 2008). Such generalisations can then be used to forecast future declines in similar taxa and regions.

One approach for estimating decline is to assess changes to species geographic ranges. This is a proxy measure for situations where any form of population monitoring, abundance data or population size estimates are not available (Telfer et al., 2002; Kotze & O'Hara, 2003; Joseph & Possingham, 2008). Species range data exists for more regions and species than population level monitoring data, providing a wider biogeographical and longer historical perspective (Dennis & Shreeve, 2003; Kuussaari et al., 2007). Although the process and mechanisms of range contractions can vary (Channell & Lomolino, 2000), it is generally accepted that reductions in range size are correlated with a decline in population size (Donald & Fuller, 1998; Shaffer et al., 1998; Telfer et al., 2002; Van Swaay et al., 2008). Thus, changes to species geographic ranges offer a less detailed but also more robust appraisal of species decline than do abundance measures (Boakes et al., 2010). The IUCN provides for geographic range contractions alone to be used as a criterion for threat status classification (criterion A2c; IUCN, 2001).

To achieve a measurement of species range change requires the comparison of two or more datasets from different time-periods. For this purpose, a recent biological atlas is often compared to historical distribution data (Rich & Woodruff, 1996; Donald & Fuller, 1998; Shaffer et al., 1998; Maes

& Van Dyke, 2001; Telfer et al., 2002; Kuussaari et al., 2007; Boakes et al., 2010; Pyke & Ehrlich, 2010). These present the most common data sources for species' past and current geographic ranges (Tingley & Beissinger, 2009; Boakes et al., 2010). Shaffer et al. (1998) term this a "sites as random effects" comparison, in which pooled records are analysed over a broad geographic area, rather than restricted to specific locations.

The data collated from natural history museums, universities and personal collections are often termed 'collections data' (Graham et al., 2004; Ferreira et al., 2007; Pyke & Ehrlich, 2010). These ad hoc data are somewhat unreliable and incomplete, but give valuable insight into the past when additional sampling is impossible (Tingley & Beissinger, 2009; Boakes et al., 2010; Pyke & Ehrlich, 2010). A biological atlas is usually a grid-based, presence-only record of species occurrence for a specific taxonomic group and region, which is collected through a systematic survey (Donald & Fuller, 1998; Dennis et al., 1999; Robertson et al., 2010). Both collections data and biological atlases are particularly vulnerable to omission errors, which in turn introduce bias into the datasets (Williams et al., 2002; Rondinini et al., 2006; Robertson et al., 2010; Botts et al., 2011).

Dissimilar sampling protocols between two datasets leads to differing degrees of omission error over time, potentially making the datasets incomparable (Donald & Fuller, 1998; Shaffer et al., 1998; Telfer et al., 2002; Dennis & Shreeve, 2003; Tingley & Beissinger, 2009). Typically, additional survey effort during recent biological surveys is responsible for higher sampling intensity in comparison to historical datasets (Romo et al., 2006). In addition, geographic and taxonomic differences between the datasets may also impede comparisons. Increased sampling effort can lead to an expansion in the geographic area covered by a survey (Ferreira et al., 2007). There may also be changes in recorder effort towards certain species. In collections data, opportunistic sampling for purposes other than documenting species occurrence can result in the overrepresentation of species targeted by historical researchers (Telfer et al., 2002; Pyke & Ehrlich, 2010). Updates to species status or taxonomy may lead to changes in sampling effort toward some species during the more recent survey (Rich & Woodruff, 1996; Telfer et al., 2002).

The measurement of the size of species geographic ranges, and by implication, the measurement of range changes over time, is dependent on sampling intensity (Rich & Woodruff, 1996; Shaffer et al., 1998; Dennis et al., 1999; Ferreira et al., 2007; Kuussaari et al., 2007). When sampling intensity is low, species are detected mainly in accessible areas where they are locally abundant (Gaston & Rodrigues, 2003). Low recording probability occurs in areas of low abundance, usually on the periphery of species ranges. Thus, range sizes tend to be under-estimated (Gaston & Rodrigues, 2003). When comparing datasets of different sampling intensities, the apparent changes to the size of species ranges may be a consequence of disparate sampling effort rather than a real phenomenon. If the sampling intensity for the second database is greater, the ranges of species may seem to be expanding (Ferreira et al., 2007).

Species occupancy models' are one approach that has been developed to reduce problems of false absences by incorporating detection probability. These models call for repeated surveys at the same location ('sites as fixed effects', Shaffer et al., 1998) (Tingley & Beissinger, 2009). Neither historical collections data nor recent atlas data are likely to fulfil this requirement. Similarly, species niche modelling is often used to improve the quality of species distribution data. However, as niche modelling is generally restricted to available abiotic variables, species ranges are frequently over-estimated (Pyke & Ehrlich, 2010), especially when using presence-only datasets (Tingley & Beissinger, 2009). Thus, primary data, showing evident changes to species ranges (Boakes et al., 2010) often holds a greater weight of proof for species declines than do probable or predicted range changes.

Consequently, only various provisional methods are available to facilitate the empirical comparison of historical datasets with recent surveys. In this paper, we aim first to apply a virtual ecologist approach to evaluate these methods (Zurell et al., 2010). We will generate hypothetical ranges that are similar to real South African amphibian ranges, but with known range change and simulated sampling. This will allow the assessment of which of these methods is best applied to detect range changes for species of the *South African Frog Atlas Project*.

3.2. Materials and methods

The *South African Frog Atlas Project* (*SAFAP*) assembled data on past and current frog species ranges in South Africa, Lesotho and Swaziland (Minter et al., 2004). Museum records, personal databases and literature reports contributed to the historical sampling period (1905 – 1995). The recent sampling period (1996 – 2003) consisted of a systematic survey of amphibians, in which presence records were collected based on either visual or audio evidence. For both sampling periods, records were generalised to a Quarter Degree Grid Cell (QDGC) resolution.

The correction methods used to ensure that current species distributions are comparable with historical data generally fall into three main groups: categorical comparisons, sub-sampling and correction factors (Table 1). We endeavoured to select methods that would be most suitable for application to datasets similar to the *SAFAP*. The central attributes of such datasets are that they are broad scale, grid-based, presence-only datasets, in which sites are random effects and all species from a certain taxonomic group are included. Two successive datasets with differing sampling protocol are generally compared, but no measure of sampling effort is available. We restricted the analysis to methods that are directly applicable to empirical data, with no requirement for additional environmental data or modelling. We chose methods specifically tailored to estimating overall range size change, rather than range shift. In selecting the specific studies that we have used as examples of each approach, we chose those that either presented new methods or had detailed methods descriptions. Particularly for the sub-sampling approach, we have selected only a representative sample of many variants in which differing sub-sampling procedures are employed. We first applied each method to a separate set of hypothetical ranges to test their effectiveness against known range changes. We then estimated the unknown range changes of *SAFAP* species using the same methods.

Table 1: References for the methods included in the comparison, divided into the three main groups. The 'Name' is the abbreviation by which each method is subsequently referred.

Group	Name	Reference	Taxon	Location
Categorical comparisons	CC1	Van Swaay (1990)	Butterflies	Netherlands
	CC2	Van Calster et al. (2008)	Vascular plants	Thiérache, France
Sub-sampling	SS1	Warren et al. (2001)	Butterflies	Britain
	SS2	Maes and Van Dyke (2001)	Butterflies	Flanders, Belgium
	SS3	Kuussaari et al. (2007)	Butterflies	Finland
Correction factors	CF1	Rich and Woodruff (1996)	Vascular plants	England & Scotland
	CF2	Telfer et al. (2002)	Plants/ Carabid beetles	Britain

3.2.1. *Hypothetical ranges*

A simple virtual ecologist approach was used to evaluate and compare the performance of the various methods (Zurell et al., 2010). The virtual ecologist approach first simulates an ecological dataset that is similar to a real situation, but with known parameters. In this case, we generated 18 hypothetical ranges with known changes. Then, simulated sampling of this virtual database imitates the real-world data collection procedure (Zurell et al., 2010). The known changes of the hypothetical ranges allowed the evaluation of each method for determining the correct sign and magnitude of range change.

We endeavoured to make the hypothetical ranges as similar as possible to existing *SAFAP* species ranges. The sizes of the historical hypothetical ranges followed the same range size distribution of the *SAFAP* species. We assigned two ranges (11.1%) only a single QDGC. Five ranges (27.8%) were between 2 and 10 QDGCs, seven ranges (27.8%) between 11 and 100 QDGCs and four ranges (22.2%) between 100 and 300 QDGCs. A central QDGC was randomly allocated to each of these ranges, within the area of known *SAFAP* species occurrence. Historical ranges of the prescribed size were constructed around this central QDGC.

The hypothetical historical ranges were then modified to generate hypothetical recent ranges. Six ranges were randomly assigned as contracting and six ranges as expanding. To simulate these changes, we either removed QDGCs from the historical ranges or added additional QDGC presence records. A 60% range change was employed for both expanding and contracting ranges. A 60% contraction in range size would result in an 'Endangered" classification if the decline occurred within the last 10 years (IUCN, 2001; Joseph & Possingham, 2008). Six ranges remained stable and their historical and recent extent was the same.

We then simulated sampling, with an increase in geographic coverage and an increase in sampling intensity. The historical ranges were clipped to within the historical coverage of the *SAFAP*, and recent ranges were clipped to the atlas coverage of the *SAFAP*. A previous analysis had assessed geographic sampling bias in the *SAFAP*, and divided QDGCs into well-sampled, possibly under-sampled and probably under-sampled cells (Botts et al., 2011). Possibly under-sampled grid cells were those with fewer than 50% of the species recorded in a well-sampled grid cell with a similar climate. Probably under-sampled grid cells also had fewer than 50% of the species in a benchmark grid cell, but also had higher topographical heterogeneity (Robertson & Barker, 2006; Botts et al., 2011). The proportions of each of these types of QDGC were calculated for all 18 hypothetical ranges. During the historical sampling period, well-sampled QDGCs were made to yield a presence record 85% of the time. Both types of under-sampled QDGCs had a 40% chance of yielding a presence record. To generate an increased sampling effort, these probabilities were increased when simulating the recent sampling. Well-sampled cells increased to a 90% detection probability. Possibly under-sampled cells now produced a 60% chance of a presence record, and probably under-sampled QDGCs, 50%. This resulted in the hypothetical ranges having similar overall proportions of these sampling quality types as the *SAFAP*, effectively recreating both the geographic and temporal sampling bias.

3.2.2. *Categorical comparisons (CC)*

In categorical comparisons, primary distribution data from one or more time-periods are categorised according to the size of a species range and scaled from rare to common. Species that have become more 'rare' over time are declining, whilst those that become more 'common' are expanding. Computing the rarity class for each species as a proportion of only those grid cells sampled during each period equalises sampling effort over time.

CC1: Van Swaay (1990) introduced a method of categorical comparison that required the separation of occurrence records into multiple five-year periods. Following Van Swaay (1990), we divided the South African frog occurrence records into 12 8-year periods, beginning in 1908 and ending with the atlas period from 1996 to 2003. We chose the 8-year periods to ensure that the recent, distinct atlas period remained undivided. For each time-period, the spatial extent of sampling was the number of grid cells containing at least one presence record of any species. The number of occupied grid cells, as a proportion of the spatial extent, gave the range size for each species at each time-period. Range size was categorised into one of nine exponential rarity classes given by Van Swaay (1990). To provide a quantitative comparison of this method with others, we slightly expanded this method by adding a trend analysis (McCarthy, 1998). For each species, we performed a Spearman correlation between the range size categories and the numbered eight-year time periods (McCarthy, 1998). This addition resulted in the exclusion of *SAFAP* species sampled in two or fewer time-periods. For the hypothetical ranges, with only two simulated time-periods, we abandoned the trend analysis and simply calculated the proportion change in rarity classes.

CC2: Categorical comparisons also facilitate the comparison of a recent survey with a historical flora or faunal account. Van Calster et al. (2008) utilised a 19th century flora of the Thiérache region of France, containing only a descriptive account of species rarity, and compared it to a recent digital database of plant records. To obtain an admittedly crude estimate of species range change, they downgraded the recent survey into classes comparable with the descriptive account (Van Calster et al., 2008). Their rarity index was also exponential, but differed from the Van Swaay (1990) method in that it had only six categories and used the proportion of unoccupied cells as a measure of rarity per species. Absences were assumed in grid cells that had been sampled, but had no presence records for the species in question. We included only grid cells sampled during both periods and calculated the proportion of unoccupied grid cells for each. Species from both the historical and atlas components of the *SAFAP* were assigned to the rarity classes. We calculated proportional range change as '*rarity class atlas /rarity class historical − 1'*.

3.2.3. *Sub-sampling (SS)*

Sub-sampling methods address differences in sampling effort by the removal of some data. The number of database records is related to the intensity of sampling. Thus, equalising the number of database records between sampling periods is a simple way of standardising sampling effort. In all cases of sub-sampling, the procedure is similar: first remove data according to a set of criteria, then calculate species range sizes based on the reduced dataset and compare them. The criteria for sub-sampling can include either random or systematic removal of database records, grid cells or species.

SS1: Warren et al. (2001) randomly sub-sampled a recent dataset to equate with the lower sampling effort of a previous sampling period. Sub-sampling was performed separately in 100 km grid squares to maintain geographic coverage. In applying this method to the *SAFAP*, we divided the database records into 45 two-degree cells and counted the number of historical records within each of these cells. Spatial variation in the distribution of records meant that the chosen two-degree grid was the smallest grid size for which the atlas period consistently had more records than the historical period. The atlas dataset was then randomly sub-sampled such that it contained exactly the same number of records as the historical period, distributed in a similar spatial pattern. Range size was the number of occupied QDGCs per species, per time-period, and range change was the proportional change in range size: '*number of historical grid cells occupied/number of atlas grid cells occupied − 1*'. Warren et al. (2001) suggested that calculating the change in the square root of area might be more appropriate, but later found that this differed little from proportional change. We retain the use of simple proportional change to ensure comparability between the various methods of sub-sampling. This method could not be applied to the hypothetical ranges, as individual frog records were not simulated.

SS2: Further sub-sampling methods restrict assessment of range change to intensively sampled grid cells. This requires an estimation of which grid cells qualify for inclusion. Maes and Van Dyke (2001) proposed that only those cells in which the most common species were detected could be considered well sampled. They restricted analysis of range change to the records found in grid cells containing all of the six most common butterfly species. This method, as in previous cases, had to be adapted for use in the *SAFAP*. We selected the six species with the largest atlas ranges, which were among the nine most common historical species. Since South Africa is larger than the study area of Maes and Van Dyke (2001), it falls within two biogeographic sub-regions. Species common to the eastern sub-region are generally absent in the west and vice versa. Thus, including only grid cells with all six of these species would have restricted the analysis to the transition zone between the sub-regions. Therefore, we broadened the criteria to include grid cells with four of the six common species. Maes and Van Dyke (2001) found that broadening the criteria thus did not materially alter their results. Records from grid cells that did not contain at least four of the six species were excluded. Range change was calculated as previously for comparative purposes, although Maes and Van Dyke (2001) preferred to use the difference between the logarithms of range size.

SS3: The degree of sub-sampling can be extensively varied, giving differing results (Kuussaari et al., 2007). It is thus prudent to attempt several different levels of sub-sampling before deciding which best suits the data and purpose. Kuussaari et al. (2007) calculated species range change from four different subsets of a Finnish butterfly atlas, with subsets restricted to grid cells with >1, >10, >40 and >100 records in all sampling periods. Overall, about 150 000 butterfly records were available before sub-sampling. Only circa 42 000 records were available in the *SAFAP* dataset. Thus, we halved the limit values used by Kuussaari et al. (2007) and restricted the subsets to those grid cells containing >1, >5, >20 and >50 records. Proportional change in the size of species ranges was calculated for each subset of the data. When applying sub-sampling to the hypothetical ranges, we restricted the analysis to the same grid cells that were identified for the *SAFAP*.

3.2.4. *Correction factors (CF)*

Correction factors involve the use of a mathematical or statistical correction to reduce differences in sampling intensity between two time-periods. They use theoretical assumptions to describe and enumerate the effects of sampling effort, and then alter range size estimates accordingly.

CF1: The correction factor of Rich and Woodruff (1996) takes the form: $R = CA + (1 - C).(A^2/n)$, where C is a constant correction factor, A is the original measured range size of each species and n is the total number of grid cells sampled. R is the relative frequency of species presence, i.e. the adjusted range size estimate. This correction factor was applied to the historical hypothetical ranges, and then to the historical *SAFAP* species ranges, to make them comparable to those of the recent survey. We only included grid cells sampled at least once during both time-periods. To determine C, we summed the range sizes of all species for the atlas period. We then applied the correction and adjusted C such that this sum for the historical period equalled that of the atlas period. Range change was proportional as before.

CF2: Telfer et al. (2002) developed the definitive statistical correction factor. This procedure assumes that changes in sampling intensity will affect the recording probability of all species in a similar manner (Telfer et al., 2002). Thus, the relationship between species range sizes during the two sampling periods can be described using a simple linear regression (Telfer et al., 2002). In applying this method to the *SAFAP*, we again included only those grid cells sampled during both time-periods. Species with fewer than five presence records in the historical period were also excluded to reduce a recognised curvilinearity in the relationship between historical and atlas range sizes (Telfer et al., 2002). We calculated the proportion of occupied grid cells for each species in each time-period and subjected them to a logit transformation to achieve normality. The transformed proportions for the historical and atlas data were then regressed against each other. The studentised residuals gave the range change index for each species. Telfer et al. (2002) found that some datasets showed heteroscedasticity. As the *SAFAP* dataset showed a slight increase in variance at lower range size proportions, the recommended weighting technique described in Telfer et al. (2002) was followed.

3.2.5. *Comparison of methods*

The range change estimates produced by each of the methods were initially compared to the known range change for each hypothetical range. We counted the number of times each method detected the correct sign (positive/negative) of change. Ranges were then divided into expanding, contracting and stable, as well as small, medium and large. The number of correct estimates of the sign of change for each of these groups was identified. We also calculated how well each method estimated the magnitude of range change. If the estimate of range change was within 0.1 of the real range change for the hypothetical ranges then it was considered a correct measurement.

For the *SAFAP* analysis, we enumerated the number of expanding, contracting and stable species for each method and compared them. Minimal range increases and decreases are not meaningfully different from stable. Hence, stable ranges were classified as those with range change between −0.1 and 0.1. Expanding species were those with a positive range change over 0.1 (or a larger than 10% increase in range size). Contracting species had a negative range change less than −0.1 (10% decrease in range size).

For each sub-sampling method, we recorded the numbers of *SAFAP* records removed from the dataset. All sub-sampling methods used comparable proportions to estimate range change. The number of records removed was contrasted with average range change to assess how measured range change is dependent on the extent of sub-sampling.

Finally, we used a cluster analysis to classify all the range change methods into groups with similar range change estimates for *SAFAP* species. To initiate this comparison, all range change estimates were standardised to normal distributions (Quinn & Keough, 2002). The analysis was limited to only those species (80) that had a range change estimate for all of the methods. Wards hierarchical cluster analysis was applied to the standardised data, and clusters were identified based on meaningful differences between the methods.

3.3. Results

3.3.1. *Hypothetical range change*

The actual average range change for the hypothetical ranges was 0.009, as six ranges were expanding and six contracting by similar proportions (a range size change of 0.6). However, after the simulated increase in sampling intensity, the average proportional range change was 0.307. This indicated a 30.7% increase in measured range size between the two sampling periods.

Even when no corrections were applied, the sign of change was accurately determined for 11 (61%) ranges (Table 2). However, expanding and stable range change proportions were overestimated on average by 0.505 and 0.306 respectively and contracting ranges underestimated by 0.296 (Figure 8). Both of the categorical comparisons and the two most severe sub-sampling methods performed worse than the uncorrected data (Table 2; Figure 8). The categorical methods underestimated all types of range change (Figure 8). The CC2 method resulted in stable range change estimates for all hypothetical ranges, and was thus correct only in the six cases when this was true (Table 2). The severe sub-sampling methods, SS3(>20) and SS3(>50), gave mostly inaccurate range change estimates and successfully calculated the sign of change for fewer than five (28%) ranges. They performed particularly poorly for small ranges (correct for less than 14%) and contracting ranges (less than 17%; Table 2).

Table 2: The percentage of hypothetical ranges for which each method correctly estimated the sign (contracting, expanding or stable) and magnitude of range change. The methods are sorted in descending order according to the percentage of hypothetical ranges for which they correctly estimated the sign of range change. Values shown in bold equal or exceed those calculated before any corrections.

Method:	**Correct sign (%)**							**Correct magnitude (%)**
	All	**Contracting**	**Expanding**	**Stable**	**Small**	**Medium**	**Large**	**All**
CF1	**83**	**100**	**83**	**67**	**71**	**86**	**100**	**50**
SS2	**78**	**83**	67	**83**	**57**	**86**	**100**	**33**
SS3(>5)	**72**	**83**	**83**	**50**	**71**	**71**	**75**	**28**
SS3(>1)	**67**	**100**	**83**	**17**	**71**	**71**	**50**	**28**
CF2	**61**	67	**83**	**33**	29	**86**	**75**	**17**
No corrections	**61**	**83**	**83**	**17**	**57**	**71**	**50**	**17**
CC1	56	67	17	**83**	43	57	**75**	**28**
CC2	33	0	0	**100**	29	29	**50**	**33**
SS3(>20)	28	17	33	**33**	14	29	**50**	**17**
SS3(>50)	11	0	17	**17**	0	29	0	6

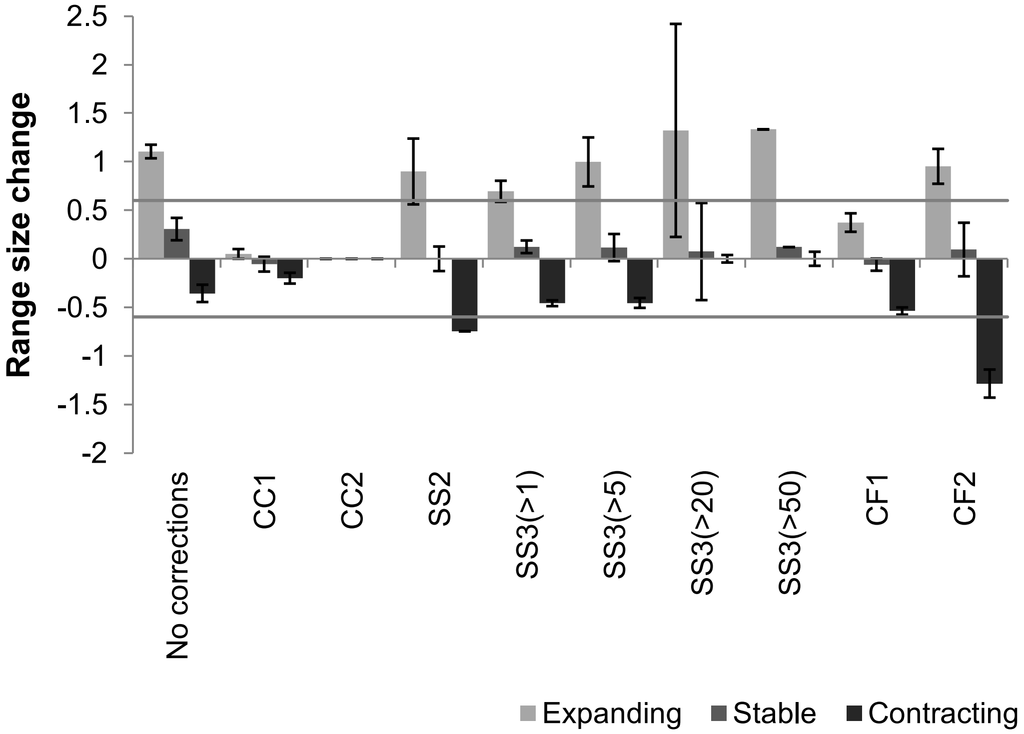


Figure 8: The mean (± standard error) measured range change for expanding, stable and contracting ranges according to each method. The guidelines at 0.6 and -0.6 show the known range change for expanding and contracting ranges.

The five other methods equalled or exceeded the performance of the uncorrected data. SS2 and CF2 generally overestimated both range expansions and range contractions (Figure 8). However, SS2 was correct at estimating the sign of range change for 14 (78%) species and performed particularly well at correctly identifying stable ranges (83% correct; Table 2). The sign of range changes for large ranges was always correctly estimated when using the methods of SS2 and CF1. These methods were also good for mid-sized ranges (86% correct), but SS2 correctly identified the sign of change for fewer than 57% of small-range species (Table 2). SS3(>1), with minimal sub-sampling, was generally unsuccessful at identifying stable ranges (only 17% correct) or estimating range change for large ranges (50% correct; Table 2). For small-range species and range contractions, the methods CF1, SS3(>1) and SS3(>5) performed well (Table 2). Of these, CF1 was the best all-round method. It correctly estimated the sign of range for 15 (83%) of the hypothetical ranges. Although CF1 was one of the few methods that underestimated range expansions (by 0.227 on average; Figure 8), it still correctly identified 83% of expanding ranges (Table 2). CF1 was certainly the best method for measuring the magnitude of range change, as it was correct to within 0.1 for nine ranges (50%; Table 2).

3.3.2. *Range change in SAFAP species*

The historical period of the *SAFAP* collected 16 975 records in 91 years, but the much shorter, eight-year atlas period amassed 25 470 records. An additional 455 QDGCs were sampled during the atlas period, improving spatial coverage of the study area from 62% to 84%. Despite the vast increase in the number of records and the extended geographic coverage during the atlas sampling-period, 96% of described species were recorded in both time-periods. The increased sampling effort of the atlas period resulted in an apparent increase in the average range size of *SAFAP* species. Several of the comparative methods confirmed this fact. Proportion change, with no corrections, resulted in an average range change of 0.268 (±0.106), or a 26.8% increase in range size. The constant correction factor (*C*) of CF1 was 1.332, indicating that range sizes in the earlier period had to be adjusted by 33.2% to be equivalent to the later period.

Despite this overall increase in average measured range size, there was still a large proportion of contracting species in the *SAFAP*. Even before any corrections were applied, proportional range change indicated that 44 (38.9%) species decreased in range size between the historical and atlas periods (Figure 9). Other estimates of the number of contracting species varied widely, from only six species (5.3%) using the CC2 method, to 68 species (60.2%) according to CF1. Simple proportional change before any corrections yielded the highest number of species with range expansions (54 species, 47.8%, Figure 9). CC2 classified most ranges as stable, and identified only 18 (15.9%) of species as expanding.

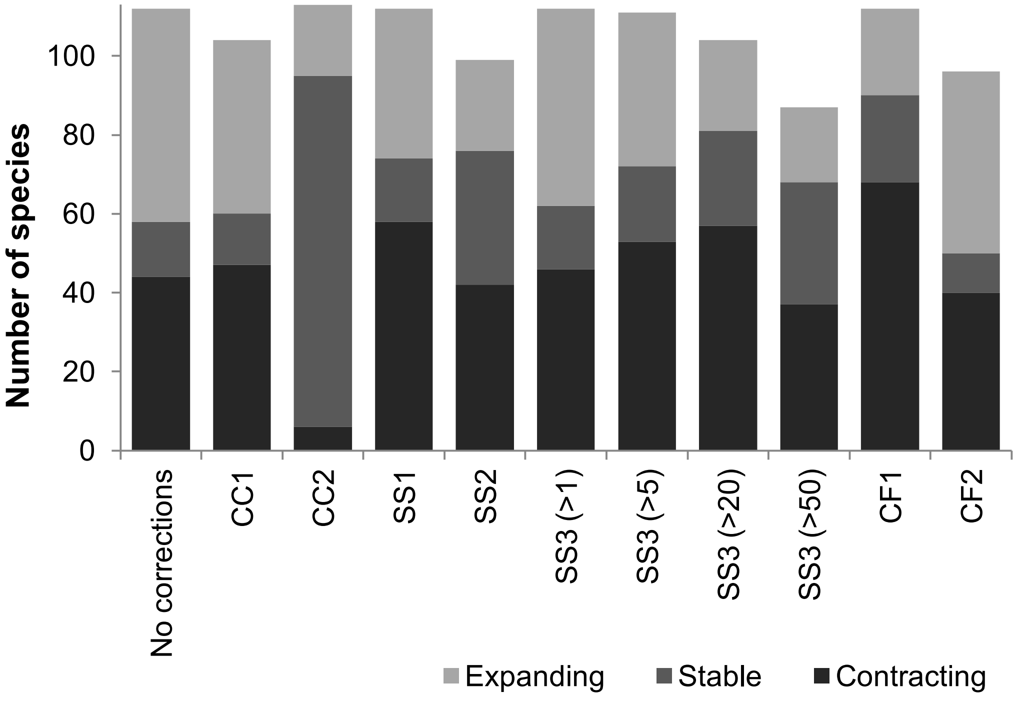


Figure 9: The number of expanding, stable and contracting species per method for the *South African Frog Atlas Project*.

Sub-sampling methods manage the reduction of spurious range expansions by excluding data. With no data removal, the average proportional range change was 0.268 (±0.106) (Figure 10). The omission of 3 315 records (SS3(>1)) reduced average proportional range change to 0.112 (±0.076). Moderate sub-sampling, approximately 8 000 – 11 500 records removed (between 20% and 27% of records), was prescribed by the SS1 and SS3(>5) methods. The average range change for these moderate sub-samples was minimally negative: −0.040 (±0.073) and −0.016 (±0.065) respectively (Figure 10). Severe sub-sampling excluded over 26 000 (61%) of the *SAFAP* records. This substantial reduction in the dataset resulted in negative average range change between −0.097 (±0.048) and −0.141 (± 0.045) (Figure 10). Removal of records also resulted in the elimination of species from the dataset. SS2 excluded 14 species (12.4%), while the most extreme sub-sampling (SS3(>50)) resulted in 26 species (23.0%) being excluded (see Figure 9). The majority (73.1%) of the omitted species had small ranges.

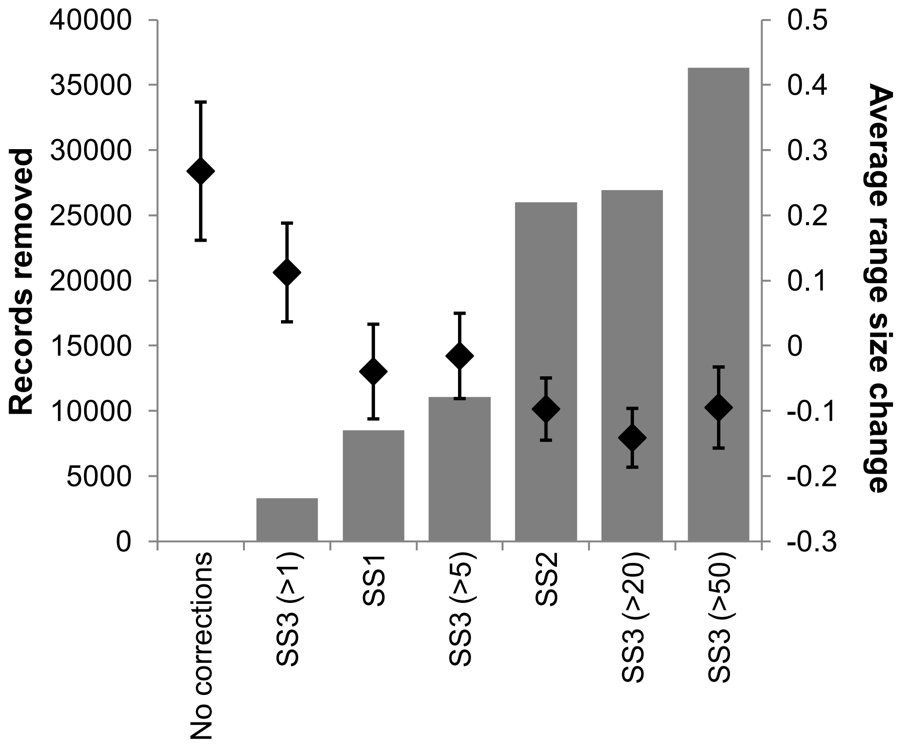


Figure 10: The number of records removed during sub-sampling methods (bars), and the average proportional range change (diamonds: mean ± standard error).

Hierarchical cluster analysis showed five feasible clusters amongst the range change methods (Figure 11). The squared multiple correlation (R^2) for these five clusters was 0.827, indicating that this cluster organisation accounted for 82.7% of the variance between the methods. Both of the categorical comparative methods were sufficiently different for each to remain as separate clusters (Clusters 3 and 5; Figure 11). The most severe sub-sampling method (SS3(>50)) also formed its own cluster (Cluster 4; Figure 11). The remaining eight methods constituted the other two clusters. Cluster 1 contained the range change estimate made before any corrections. Four other methods were similar enough to this unprocessed range change estimate to be included in the same cluster. Sub-sampling methods that removed fewer than 27% (11 500 records) of the data and CF1 were included in Cluster 1 (Figure 11). Cluster 2 contained the more severe forms of sub-sampling in which more than 61% (26 000 records) of data was removed, as well as CF2 (Figure 11).

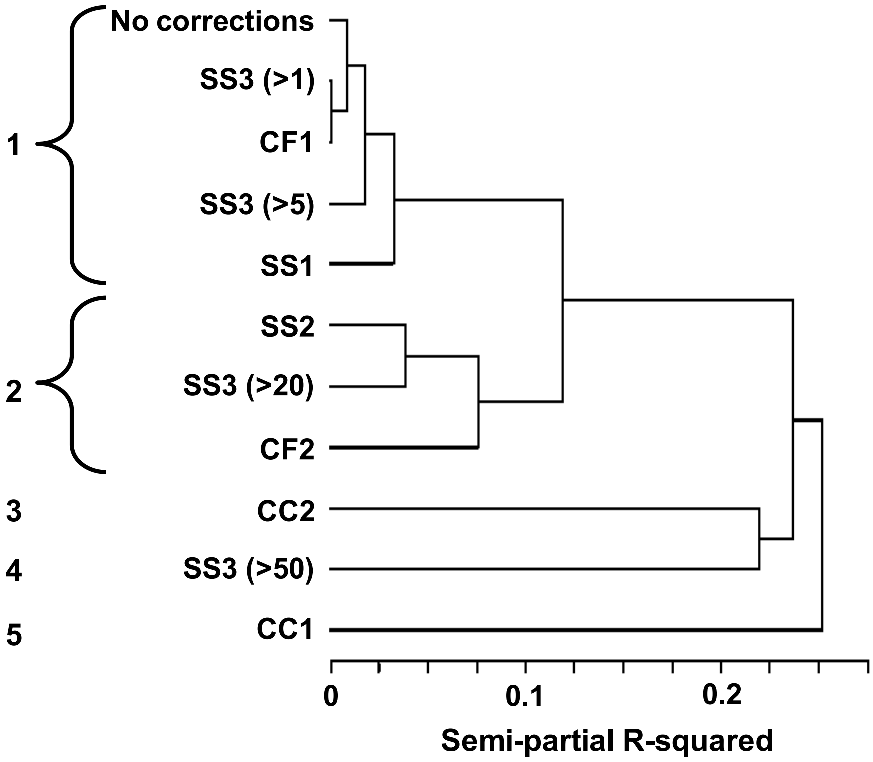


Figure 11: Cluster diagram showing the results of the hierarchical cluster analysis. Numbered labels indicate membership of the five clusters.

3.4. Discussion

Uncorrected measures of *SAFAP* species range sizes showed range expansions of approximately 30% after 1996. This is unlikely to be a real biological phenomenon and is doubtless a symptom of differences in sampling strategies between the historical and atlas datasets. Erroneous increases in measured range sizes result from an increase in sampling intensity over time (Ferreira et al., 2007; Kuussaari et al., 2007). This is a typical issue, which frequently limits the comparability of historical and recent surveys (Rich & Woodruff, 1996). Decreases in sampling intensity over time would cause the opposite problem: an apparent contraction in range size over time. Similar methods could be used to correct decreased sampling intensity, but as this problem is uncommon and did not apply to *SAFAP*, we have not tested their efficacy here.

Increased sampling intensity over time resulted in an improved geographic coverage of the *SAFAP* study area. The historical dataset is the only available baseline for past ranges of South African amphibians. However, it is limited in coverage to only 62% of the total area of South Africa. A 22% increase in geographic coverage during the atlas sampling-period means that species appeared to expand their ranges into newly sampled regions. All of the methods we reviewed here made some provision for managing changes in geographic coverage. Most did this by limiting the dataset to those areas covered during both sampling periods. This precaution unfortunately restricts the scope of the analysis to within the smaller geographic area, but it also effectively controls the effects of change in coverage.

Another consequence of increased sampling intensity is the concurrent rise in detection probability. Intensified sampling effort leads to a greater likelihood that researchers detect and record species in areas of lower abundance. The atlas period of the *SAFAP* produced substantially more records (1.5x more) than the historical period, during a much shorter time-period. The higher detection probability during the atlas period will thus have resulted in the larger measured range sizes and apparent range expansion over time. Detection probability is intrinsic within the dataset, and is based on many confounding factors that vary over space and time (Tingley & Beissinger, 2009). Thus, the magnitude and effects of increased detection probability are more difficult to quantify and control than those of geographic coverage. The various methods reviewed here take different approaches to handle the effects of increased recording probability, with varying success.

Without correction for the 22% increase in geographic coverage, and the 1.5x greater sampling intensity, range change measures in the *SAFAP* may have been overstated by as much as 30%. In this scenario, expanding species will appear to have increased by an exaggerated degree. Species with real minimal range contractions, or stable species, may also wrongly classify as expanding. Despite this, many *SAFAP* species (38.9%) still showed negative proportional change. Any species with negative measured range changes after increased sampling are likely to be undergoing real range contractions. Thus, in the usual case of intensified sampling over time, sizable range contractions can be more reliably documented than range expansions (Dennis & Shreeve, 2003), although these range contractions are almost certainly underestimated. For this reason, the uncorrected data provided a reasonable estimate of the sign of range change, but it was among the worst methods for correctly estimating change in stable species or the magnitude of change.

Categorical comparative methods were developed to make full use of early, descriptive natural history assessments. Written ‘floras’ and ‘faunas’ are a potentially worthwhile source of historical data. Categorical comparisons may hold an essential function within this context. However, the process of downgrading quantitative data into categories results in a loss of precision and an inferior assessment of range change. The categorical comparative methods were notably different from all other methods and each other in their assessment of range change for *SAFAP* species. They both also performed poorly in estimating the sign and magnitude of change for the hypothetical ranges.

The results of CC1 were generally superior to those of CC2, correctly identifying the sign of range change for more species on most counts. Only for stable ranges did CC2 surpass CC1, primarily because CC2 classified all hypothetical ranges as stable. These differences between the methods highlight the effect of different threshold values for rarity classes. Proportional changes to small ranges necessarily involve fewer grid cells than a similar proportional change in large ranges and rarity classes must account for this. The rarity classes for both methods were structured exponentially, but CC1 had more classes and began with narrower categories for smaller ranges than did CC2. The broader rarity classes of CC2 meant that even the simulated 60% range changes did not cause a change in category. Van Calster et al. (2008) (CC2) went on to refine their method by reversely converting the categorical data into quantitative data and then applying CF2. Other authors have also made similar additions to categorical comparisons. McCollin et al. (2000) performed a linear regression between historical range size categories and recent range size measurements.

At a minimum, sub-sampling procedures account for changes in geographic coverage by limiting analysis to grid cells sampled in both time-periods (as in SS3(>1)). The importance of this nominal correction was emphasised as the average measured range change of *SAFAP* species more than halved (from 0.268 to 0.112) after it was applied. Any further sub-sampling aims to control for different recording probability between the time-periods. SS1 achieved this by equalising the numbers of records. Other sub-sampling methods restrict analysis to only well-sampled grid cells. Detection probability in well-sampled grid cells should be sufficiently high that most species present are recorded. This further sub-sampling resulted in an average measured range contraction of *SAFAP* species. Sub-sampling methods thus call for a balance between the proportion of data removed and the reduction of false range expansions. The moderate sub-sampling methods of SS1 and SS3(>5) were successful in achieving this balance, and consequently correctly deduced the sign of change for most hypothetical ranges. Only stable ranges were still sometimes overestimated, and the more severe sub-sampling of SS2 was better able to identify stable ranges. Severe sub-sampling can be so limiting to the dataset that few species and records are left to provide a realistic assessment of range change. Few records, grid cells and species remained after the rigorous sub-sampling of SS3(>50). This measure of change was significantly different from all other methods for the *SAFAP* dataset, and performed the worst in estimating either the sign or magnitude of change in hypothetical ranges.

Sub-sampling methods have one important advantage over other methods. Both the categorical comparisons and correction factors utilise the total range size measures for each species. This total range size measure is the sum of all grid cells in which the species is present. If sampling intensity corrections are only made to this summarised value, then the underlying species presence records will retain the sampling intensity effects. This is critical for subsequent spatial analyses of the data at the species level. Only sub-sampling methods directly correct for sampling intensity differences within the individual species presence records. Thus, while other methods may be superior for overall range change estimations, sub-sampling methods should always precede spatial investigations of species ranges to reduce sampling intensity effects. For this reason, the evaluation by Hassal and Thompson (2010) of similar methods for detecting directional range shifts is primarily restricted to sub-sampling methods. Their conclusion that SS1 is the optimal method for detecting range shifts is consistent with our analysis, which placed SS1 in Cluster 1 with other methods that performed well in estimating range size change.

Correction factors begin with the restriction of records to within the spatial extent of shared geographic coverage between the time-periods. Other than this, they manage differing sampling intensity with minimal removal of data. Correction factors are thus preferable to sub-sampling methods as they retain valuable records that would otherwise be discarded. Both correction factors performed well at identifying the sign of change, although CF1 equalled or slightly exceeded CF2 in most aspects. For the *SAFAP*, CF2 was more closely aligned with the more severe sub-sampling methods. It also showed similar results to these methods for the hypothetical ranges, having generally overestimated range change and poorly identified change in small ranges. Conversely, it efficiently dealt with false range expansions, and generally classified medium and large expanding ranges correctly. The change index of this statistical correction factor was, however, poor at estimating the magnitude of change. McCollin et al. (2000), who used a similar linear regression, speculate that residuals may not represent the true magnitude of species range change, but may only show the broad trend in change direction. CF1 was good at identifying the sign of change in hypothetical ranges, and by far surpassed other methods for magnitude of change, achieving 50% accuracy.

Most methods showed an anomalous result for a small number of species that were only recently described. This is evidence of a taxonomic bias in which there was a change in recorder effort towards these species between the two datasets (Telfer et al., 2002). Four species that were described since 1993 had outlying range change estimates larger than one according to CF1, indicating a doubling (or more) of range size. Formal species descriptions allowed these species to be targeted for sampling during the atlas period in a manner that was unachievable during the historical sampling period when these species were unknown.

Hypothetical ranges were useful for assessing the relative performance of the various methods, but could not be too closely relied upon. The many variables involved in the spatial position, pattern and dynamics of real species ranges are impossible to replicate precisely (Zurell et al., 2010). However, the hypothetical ranges provided an indication of the strengths and weaknesses of the various methods. This enabled an informed assessment of which clusters of methods were most likely to correctly estimate range change in the *SAFAP*.

Cluster 1 has the most potential for providing reliable range change estimates. These methods collectively had superior estimates of the sign of range change, particularly for vulnerable small-range species and critical range contractions. Of these methods, SS3(>5), CF1 and possibly SS1 efficiently account for both increased geographic coverage and increased detection probability. The method of CF1 was the most successful, and achieved the required standard with only minor removal of data. Specifically, it attained a 100% success rate for identifying range contraction in the hypothetical ranges. Hence, it is recommended that this method is the one best applied to the *SAFAP* data. Notably, the uncorrected proportional change was also included in Cluster 1, indicating that it may be useful as a preliminary method for range change estimates, provided its limitations are clearly understood. If the methods of Cluster 1 retain some sampling intensity effects, researchers should turn with caution to Cluster 2. The methods within Cluster 2 deal more rigorously with the effects of sampling intensity, but in the process eliminate some species, particularly restricted range species. Furthermore, if the sub-sampling is too severe, results promptly become unrealistic. Of Cluster 2 methods, SS2 and CF2 are generally consistent in the correct assessment of the sign of range change. SS2 may be the preferred method for the specific task of controlling false range expansions in stable species. There may be some value in applying more than one method, or using an average from several of the more reliable approaches to provide an estimation of possible methodological variance.

The comparison of two datasets may not represent a long enough time series to unequivocally detect long-term population declines (Van Swaay et al., 2008). However, even small reductions in species range sizes could indicate substantial decreases in abundance (Shaffer et al., 1998; Kotze & O'Hara, 2003; Van Swaay et al., 2008). In the context of known environmental changes, and amphibian declines, investigations into species range contractions must occur without unnecessary delay (Tingly & Beissinger, 2009). The careful use of methods such as those reviewed here allow for biased, ad-hoc collections data to be valuable in identifying changes to species ranges (Donald & Fuller, 1998; Williams et al., 2002; Romo et al., 2006). Furthermore, the typical increase in sampling intensity over time means that important range contractions can be more reliably detected than range expansions (Dennis & Shreeve, 2003).

It is concerning that the method we recommend as most realistic for the *SAFAP* data is also the method that gave the highest number of contracting species. According to the procedure of CF1, 60.2% of all *SAFAP* species had negative range contractions lower than −0.1 (see Appendix). This number is higher than the global number of amphibian species estimated by the IUCN to be declining (42%; IUCN, Conservation International & NatureServe, 2008). South African species are generally thought to have escaped the catastrophic declines seen in the neotropics and Australia (Stuart et al., 2004). Our analysis suggests that substantial numbers of species may have experienced a reduction in range size, possibly due to a more gradual decline resulting from reduced habitat and other threats. These species are now plausible candidates for population monitoring or conservation action. Species with range contractions may qualify for formal classification in Vulnerable (30 – 50% contraction), Endangered (50 – 80% contraction) or Critically Endangered (80 – 100% contraction) categories according to IUCN criterion A2c (IUCN, 2001). Further investigations into the possible causes of these range contractions are also recommended.

3.5. References

Boakes, E. H., McGowan, P. J. K., Fuller, R. J., Chang-qing, D., Clark, N. E., O'Connor, K. & Mace, G. M. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8: e1000385.

Botts, E. A., Erasmus, B. F. N. & Alexander, G. J. (2011) Geographic sampling bias in the *South African Frog Atlas Project*: implications for conservation planning. *Biodiversity and Conservation* 20: 119-139.

Channell, R. & Lomolino, M. V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography* 27: 169-179.

Dennis, R. L. H. & Shreeve, T. G. (2003) Gains and losses of French butterflies: tests of predictions, under-recording and regional extinction from data in a new atlas. *Biological Conservation* 111: 131-139.

Dennis, R. L. H., Sparks, T. H. & Hardy, P. B. (1999) Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Donald, P. F. & Fuller, R. J. (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study* 45: 129-145.

Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Fishpool, L. D. C., Foster, M., Knox, D., Langhammer, P., Matiku, P., Radford, E., Salaman, P., Sechrest, W., Smith, M. L., Spector, S. & Tordoff, A. (2004) Key Biodiversity Areas as Site Conservation Targets. *BioScience* 54: 1110-1118.

Ferreira, D., Malard, F., Dole-Olivier, M.-J. & Gilbert, J. (2007) Obligate groundwater fauna of France: diversity patterns and conservation implications. *Biodiversity and Conservation* 16: 567-596.

Gaston, K. J. & Rodrigues, A.S.L. (2003) Reserve Selection in Regions with Poor Biological Data. *Conservation Biology* 17: 188-195.

Graham, C. H., Ferrier, S., Huettman, F., Moritz, C. & Townsend Peterson, A. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* 19: 497-503.

Hassal, C. & Thompson, D. J. (2010) Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution* 1: 343-350.

IUCN (2001) Categories and Criteria (version 3.1). Prepared by the IUCN Species Survival Commission. IUCN, Gland. http://www.iucnredlist.org/static/categories_criteria_3_1. Cited 16 July 2010.

IUCN, Conservation International & NatureServe (2008) An analysis of amphibians on the 2008 IUCN Red List. http://www.iucnredlist.org/initiatives/amphibians/analysis. Cited 18 October 2010.

Joseph, L. N. & Possingham, H. P. (2008) Grid-based monitoring methods for detecting population declines: Sensitivity to spatial scale and consequences of scale correction. *Biological Conservation* 141: 1868-1875.

Kotze, D. J. & O'Hara, R. B. (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135: 138-148.

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen, K. (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation* 11: 351-366.

Maes, D. & Van Dyke, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation* 99: 263-276.

McCarthy, M. A. (1998) Identifying declining and threatened species with museum data. *Biological Conservation* 83: 9-17.

McCollin, D., Moore, L. & Sparks, T. H. (2000) The Flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation* 92: 249-263.

Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H., Bishop, P. J. & Kloepfer, D. (eds) (2004) Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland. SI/MAB Series #9. Smithsonian Institution, Washington, DC.

Phillips, K. (1990) Where Have All the Frogs and Toads Gone? *BioScience* 40: 422-424.

Pyke, G. H. & Ehrlich, P. R. (2010) Biological collection and ecological/environmental research: a review, some observations and a look to the future. *Biological Reviews* 85: 247-266.

Quinn, G. P. & Keough, M. J. (2002) *Experimental Design and Data Analysis for Biologists* Cambridge University Press, Cambridge.

Rich, T. C. G. & Woodruff, E. R. (1996) Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217-229.

Robertson, M. P. & Barker, N. P. (2006) A technique for evaluating species richness maps generated from collections data. *South African Journal of Science* 102: 78-84.

Robertson, M. P., Cumming, G. S. & Erasmus, B. F. N. (2010) Getting the most out of atlas data. *Diversity and Distributions* 16: 363-375.

Romo, H., García-Barros, E. & Lobo, J. M. (2006) Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29: 873-885.

Rondinini, C., Wilson, K. A., Biotani, L., Grantham, H. & Possingham, H. P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136-1145.

Shaffer, H. B., Fisher, R. N. & Davidson, C. (1998) The role of natural history collections in documenting species declines. *Trends in Ecology and Evolution* 13: 27-30.

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H. & Bradshaw, C. J. A. (2008) Measuring the Meltdown: Drivers of Global Amphibian Extinction and Decline. *PLoS ONE* 3: 1-8.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. *Science* 306, 1783-1786.

Telfer, M. G., Preston, C. D. & Rothery, P. (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation* 107: 99-109.

Tingley, M. W. & Beissinger, S. R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution* 24: 625-633.

Van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M. & Decocq, G. (2008) Unexpectedly high 20th century floristic losses in a rural landscape in northern France. *Journal of Ecology* 96: 927-936.

Van Swaay, C. A. M. (1990) An assessment of the changes in butterfly abundance in the Netherlands during the 20th Century. *Biological Conservation* 52: 287-302.

Van Swaay, C. A. M., Nowicki, P., Settele, J. & Van Strien, A. J. (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation* 17: 3455-3469.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414, 65-69.

Williams, P. H., Margules, C. R. & Hilbert, D. W. (2002) Data requirements and data sources for biodiversity priority area selection. *Journal of Bioscience* 27: 327-338.

Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B. & Grimm, V.R. (2010) The virtual ecologist approach: simulating data and observers. *Oikos* 119: 622-635.

Chapter 4: Range shifts

Botts, E. A., Erasmus, B. F. N. and Alexander, G. J. Comparison between predicted and observed range dynamics of South African amphibians under conditions of global change.

4.1. Introduction

Environmental perturbations govern changes in the size, shape and location of species ranges (Brown et al., 1996; Gaston, 2003; Thomas et al., 2010) and therefore dynamic ranges are an expected response to global change. Range size changes occur when suitable conditions are either lost, or become newly available. Range shifts are characterised by a directional movement in species range. The direction and rate inherently reflect both the nature of any external environmental factors, as well as the ability of species to react. Thus, under a certain set of conditions, species range changes should be systematic and predictable (Broennimann et al*.,* 2006; Rosenzweig et al., 2007). Indeed, many predictions have been made about the possible range changes that should be expected under conditions of global change. It is highly informative to validate these predictions with observed trends. Amphibians have experienced severe population declines in recent decades (Stuart et al., 2004; IUCN et al., 2008). Contrasting predicted and observed range dynamics provides valuable clues to the principal threats faced by amphibians.

In response to changes in long-term climate means, which manifest at a broad spatial scale, species entire ranges are expected to shift along temperature and precipitation gradients. Most simply, poleward and upslope shifts are anticipated during climate warming (Parmesan et al., 1999; McCarty, 2001; Parmesan & Yohe, 2003; Root et al*.,* 2003; Shoo et al., 2006). Range shifts are one of the most common means by which species respond to climate change (Carey & Alexander, 2003; Hickling et al*.,* 2005; Hickling et al., 2006) and shifts consistent with climate change predictions have already been widely observed. Meta-analyses have indicated that approximately 80% (Parmesan & Yohe, 2003), 81% (Root et al., 2003) or 84% (Hickling et al., 2006) of assessed species have shifted in the expected polewards and upslope directions. These multi-species meta-comparisons confer higher confidence in climate change attribution than would a single-species analysis. Consistently similar range shifts between species and regions suggest that a common global factor is responsible (McCarty, 2001; Broennimann et al., 2006).

Systematic range shifts have been well documented in northern hemisphere temperate regions, and have been accepted as evidence of a general climate change response among species (Rosenzweig et al., 2007; Wright et al., 2009). However, there have been few empirical investigations confirming analogous changes in the southern hemisphere or Africa (Simmons et al., 2004; Rosenzweig et al., 2007). Several modelling and speculative exercises have detailed what range shifts to expect (Erasmus et al., 2002; Rouget et al., 2004; Simmons et al., 2004). In addition to the global-scale predictions of latitudinal and altitudinal shifts, regional topography and prevailing precipitation patterns generate more localised species responses to climate change. Under future doubled CO_2 scenarios, the climate envelopes of various southern African taxa show eastward shifts (Erasmus et al., 2002). This corresponds to a strong west-to-east aridity gradient in southern Africa (Erasmus et al., 2002). Areas of biome resilience to climate change are expected to be concentrated along the eastern and southern escarpments (Hannah et al., 2002; Rouget et al., 2004; Figure 12d), and species are expected to shift their ranges to within these areas of climate stability. Since predictions involve a substantial reduction in the area of suitable climate for most species, contractions of species ranges are also anticipated (Erasmus et al., 2002). Simmons et al. (2004) hypothesised that bird distributions would shift southwards and eastwards. However, observed changes in South African avian distributions have indicated that expansions mostly occur in a southwesterly direction, probably as a combined response to land-cover and climate changes (Okes et al., 2008; Hockey et al., 2011).

The pervasive effects of land-cover change also affect species ranges. Land-cover change acts at finer spatial scales than does climate change (Pearson et al., 2004; Virkkala et al., 2005; Broennimann et al., 2006), but it is one of the most significant drivers of past and current species range contractions (Chapin III et al., 2000; Sih et al., 2000; Warren et al., 2001; Parmesan & Yohe, 2003). Species ranges can be negatively affected by land-cover change if individuals are killed, resources reduced or habitat fragmented such that dispersal is prevented (Sih et al., 2000; Collins & Storfer, 2003; Cushman, 2006). The effects of land-cover change on species distributions are generally considered widespread and easily apparent, although few studies have demonstrated the mechanistic processes by which amphibians respond to habitat modifications (Gardner et al., 2007). Habitat destruction generally causes losses in the overall geographic area that a species occupies (Sih et al., 2000), and the effects are evident through local extinctions. This will theoretically result in an irregular loss of range, in regions where land transformation has been the most extensive (Donald & Fuller, 1998). Retraction of a species from an area of high land transformation, or expansions into newly suitable habitat, may also appear as a directional shift.

Globally, land cover change is one of the most widely cited threats to species. Habitat loss affects more than half of the amphibians species listed as Threatened by the IUCN (IUCN et al., 2008). Similarly, habitat loss is one of the most significant threats to South African amphibians (Minter et al., 2004). As of 1994/1995, 20% of South Africa's land surface was transformed (Fairbanks et al., 2000), although higher levels of transformation were concentrated in the eastern half of the country and along the coastline (Figure 12c). Urban areas, cultivation and plantations were the primary land cover types involved in land transformation (Fairbanks et al., 2000). As well as range contractions, predicted responses of South African species to land-cover change include a directional shift away from highly transformed regions (i.e. westward).

The need for a historical baseline during range change studies has led to a revived interest in long-term datasets such as museum records (Hickling et al*.,* 2006; Tingley & Beissinger, 2009). While not optimal, these datasets can be valuable in providing a historical reference point for comparisons. Museum databases are often the most comprehensive and spatially complete historical datasets (Boakes et al*.,* 2010). The historical species distributions must then be compared with a recent survey to detect changes. Changes in recorder effort and sampling protocol are a restrictive problem when comparing different datasets (Donald & Fuller, 1998; Shaffer et al*.,* 1998; Hickling et al*.,* 2005; Hickling et al*.,* 2006; Tingley & Beissinger, 2009). However, there are methods available to improve comparability of datasets and reduce the effects of sampling effort on comparisons (Botts et al., 2012).

Contrasting observed trends with predictions can identify possible drivers of species range dynamics, and contribute to the validation and improvement of global change hypotheses. Separating species responses to land cover and climate effects during natural, observational experiments is challenging (Wilson et al*.,* 2005; Broennimann et al*.,* 2006; Hickling et al*.,* 2006) and necessitates, at least, the concurrent investigation of range size changes with range shifts. We used the *South African Frog Atlas Project* to investigate recent range dynamics in South African frogs, and to relate these to land-cover and climate change predictions. Sampling biases in the dataset were accounted for, providing a reliable, quantitative measurement of range size change and range shifts for all South African amphibian species.

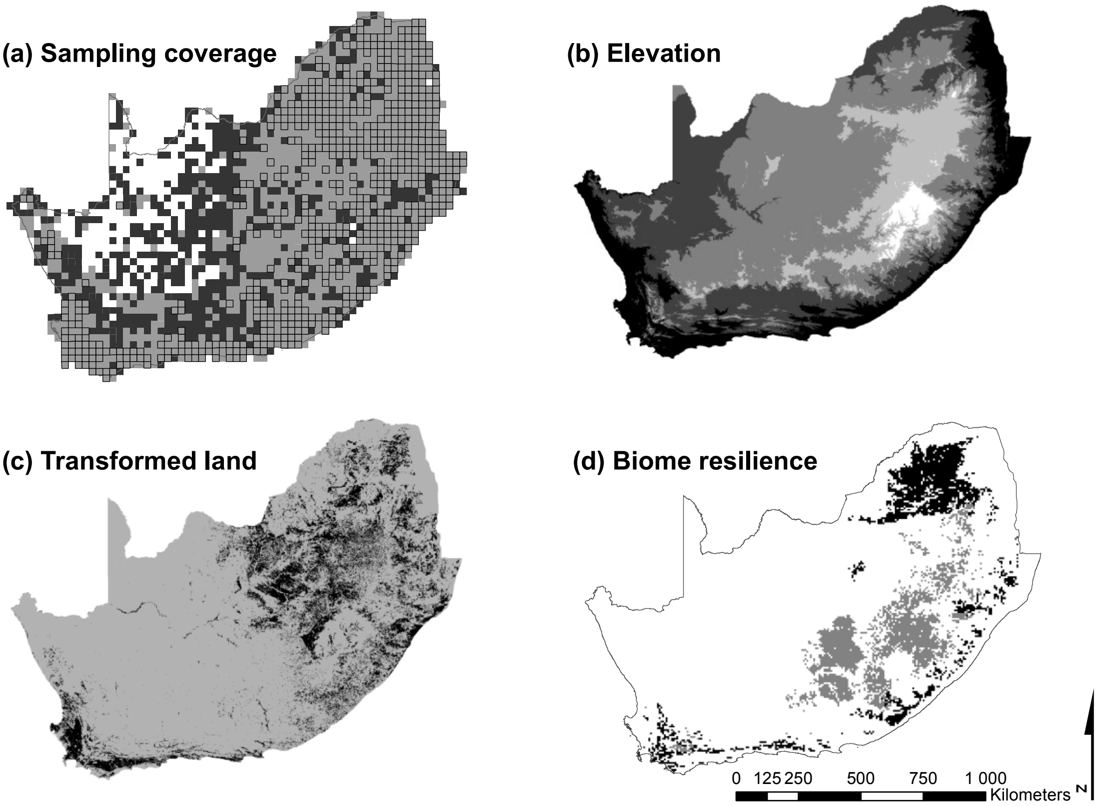


Figure 12: Maps of the study area. (a) The sampling coverage across the study area, with light grey indicating grid cells sampled before 1996, and darker grey indicating grid cells only sampled after 1996. No records were collected in the white grid cells. The QDGCs with >5 records in both time periods are shown with a black border. (b) The topography of South Africa courtesy of the Shuttle Radar Topography Mission (USGS, 2004). Black colour represents <500 m elevation, dark grey 500 – 1 000 m, grey 1 000 – 1 500 m, pale grey 1 500 – 2 000 m, white >2 000 m. (c) Transformed land (black) and natural vegetation (grey) in 1994/5 from the South African National Land-Cover database (CSIR & ARC, 1996). (d) Biome resilience to climate change courtesy of the National Spatial Biodiversity Assessment (Rouget et al., 2004; Reyers et al., 2007). The black regions highlight Savanna biome resilience in the east and Fynbos biome resilience in the west. The pale grey shows biome resilience for the Grassland, Nama-Karoo and Succulent Karoo biomes.

4.2. <u>Methods</u>

The *South African Frog Atlas Project* (*SAFAP*) amassed the most comprehensive database of past and present species distributions for amphibians of South Africa, Lesotho and Swaziland (Minter et al., 2004). Collation of museum records, literature reports and personal databases provided the historical perspective dating from 1905 to 1995. Some 16 900 historical records were retained after doubtful records were excluded and taxonomy updated. A systematic atlas survey of frogs from 1996 to 2003 provided the recent species range data. In this phase of the project, volunteers and herpetologists collected 25 000 additional species presence records based on either visual or audio evidence. Both historical and atlas datasets were compiled at the Quarter Degree Grid Cell (QDGC) resolution.

The *SAFAP*, like many other projects of this nature, was not immune to sampling biases. Records were significantly biased towards human infrastructure such as cities, roads and protected areas (Botts et al., 2011). Arid and high altitude areas were also poorly sampled (Minter et al., 2004; Botts et al., 2011). The higher sampling intensity during the later sampling period resulted in an increased geographic coverage (Figure 12a) and increased detection probability for all species. This led to an apparent expansion in average range sizes (Botts et al*.,* 2012). These problems of data quality have to be considered when using this dataset, and we have made every attempt to minimise their impact on the analyses presented here (detailed below).

Range size changes were calculated as proportional changes in the number of QDGCs occupied between sampling periods. The analysis was restricted to those QDGCs with at least one presence record in both sampling periods. This ensured that the increase in geographic coverage did not result in overstated species range expansions. To account for differing sampling intensities between the historical and atlas time periods, we applied a correction factor to the historical range sizes which improved comparability to the recent range sizes ($R = CA + (1 - C).(A^2/n)$, where C is a constant correction factor, A is the historical measured range size of each species and n is the total number of grid cells sampled. R is the relative frequency of species presence, i.e. the adjusted range size estimate; Rich & Woodruff 1996). Of several methods tested on a set of hypothetical South African amphibian ranges, this correction factor provided the most accurate measure of range change (Botts et al., 2012), and reduced spurious range increases related to increased sampling intensity. The proportional change gives the range size change, with negative values indicating contractions and positive values expansions.

Sampling biases can also be challenging when calculating range shifts. Most previous analyses of range shifts have focussed on either northern or southern range boundaries. Unfortunately, the delineation of range edges is very susceptible to changes in sampling intensity, with higher sampling intensities generally increasing the documented range size at the boundaries (Shoo et al*.,* 2006). For this reason, Shoo et al. (2006) measured altitudinal range shifts at the mean altitude, as sampling-related changes at range boundaries have little overall effect on the midpoint of the range. To minimise any further adverse sampling intensity effects, we also limited the analyses to QDGCs with more than five records of amphibian presence in both the historical and atlas time-periods (Hickling et al*.,* 2006; Shoo et al*.,* 2006). This sub-sampling method was similar, when calculating range change, to the correction factor mentioned above, but it is more appropriate for spatial analyses

(Botts et al., 2012). From 2 017 grid cells in the study area, only 603 (29.9%) of the best-sampled grid cells qualified under this criterion (Figure 12a).

We calculated the mean latitude, longitude and altitude shifts at each species range centre. This mean range centre was calculated from the centre points of all QDGCs in which the species had been recorded as present in each time-period. The difference between the two mean centres gave the distance and direction of species range shift. To calculate mean altitudinal shift, we used a 90 m digital elevation model of South Africa available through the Shuttle Radar Topography Mission (Figure 12b; USGS, 2004). This elevation dataset had a stated target for vertical error of less than 16 m, but the absolute height error for Africa has been assessed to be less than 6 m (Rodríguez et al., 2006). We calculated the mean altitude for all QDGCs in which each species was present in the two time-periods. Again, the difference between these gave the mean altitudinal shift for each species.

We related range shifts to range size changes using linear regressions (Wilson et al., 2005), with significance of the slope and intercept tested at the 5% level ($p < 0.05$). This was done to ensure that any range shifts that we calculated were independent of any changes in range size. The slope of the linear relationship signified whether range shifts were correlated with expanding or contracting species ranges. Hence, a significant slope occurs when range size changes are responsible for the variation in range shifts. The intercept of the regression line determines whether there is a general directional movement in species ranges despite any possible relationship with range size changes. An intercept significantly different from zero indicates a mean range shift independent of expanding and contracting ranges. This regression was conducted separately for mean latitude, mean longitude and mean altitude.

The distance and direction of range shifts is expected to be similar for species occupying similar biogeographic areas. Hypothesised drivers of range shift attain additional credibility when groups of species occupying similar biogeographic regions experience similar range shifts (McCarty, 2001; Broennimann et al., 2006). For this reason, species were subdivided into those indicative of each of three biogeographic districts with more than five indicator species (Alexander et al., 2004). The regressions detailed above were then restricted to species of the Bushveld District, Eastern Escarpment District and Winter/Transitional Rainfall District.

The results were limited to 100 species for which both range size change and range shifts could be reliably calculated. All analyses that use multiple species comparisons assume that species are independent data points. In some cases this may be incorrect, as species which share an evolutionary history are more likely to be similar than those that are more distantly related (Stearns, 1983; Diniz-Filho et al., 2005). To identify the effects of phylogeny on the dependence of data points, a nested ANOVA was conducted in which 'Family' and 'Genus within Family' were used as predictors of range size changes and range shifts (Stearns, 1983; Diniz-Filho et al., 2005; Cooper et al., 2008). If either 'Family' or 'Genus within Family' has significant effects on any of the variables, the residuals of the nested ANOVA can be used to isolate the specific component of variation.

4.3. Results

Taxonomic structure was not a significant predictor of range size change ($F = 1.33$; $p = 0.163$), mean longitude ($F = 1.36$; $p = 0.150$), mean latitude ($F = 1.29$; $p = 0.191$) or mean altitude ($F = 1.03$; $p = 0.445$). Thus, the phylogenetic subtraction technique was not applied and the variables were included in their original form.

Seventy of the 100 species experienced range contractions (negative range size change) after the correction factor was applied. For 17 of these species, range contractions were minimal, with proportional range size change of between 0 and -0.2. More severe range contractions, with proportional range size change < -0.2 were experienced by 53 species.

Southwards shifts were recorded for 40 species. There was no significant directional shift in mean latitude for all South African amphibians (Figure 13). When the change in mean latitude was regressed against range size change there was neither a significant slope (14 470.4 m; $R^2 = 0.02$; $p = 0.124$) nor intercept (3 976.4 m; $p = 0.358$). The non-significant slope indicates that changes in latitude where not related to range size changes: both expanding and contracting species had similar mean latitudinal movements. The intercept shows that this mean latitudinal movement of species was not significantly different from zero.

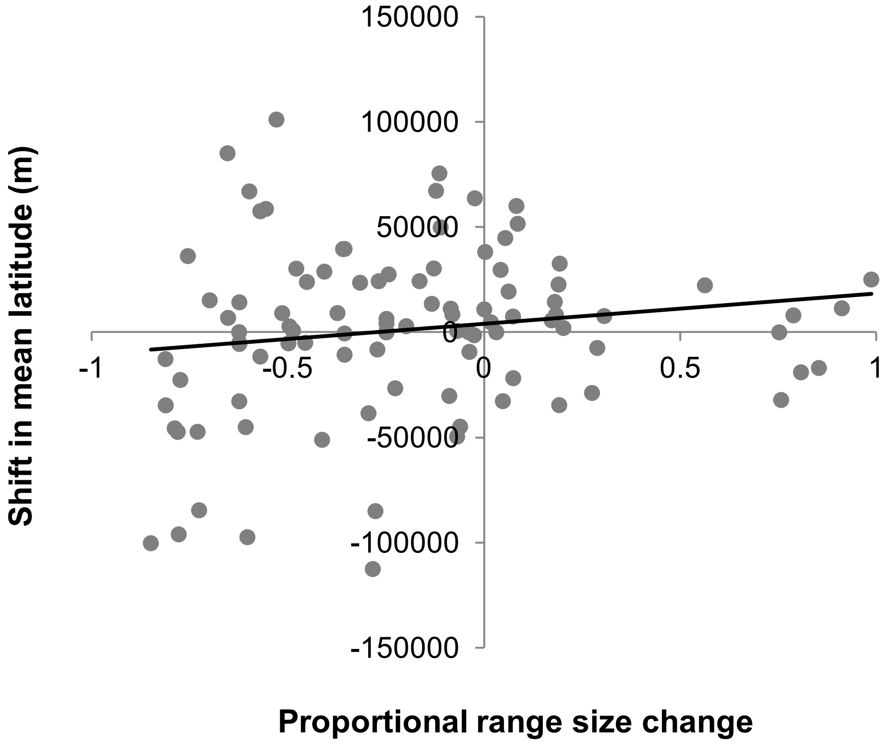


Figure 13: The shift in mean latitude (m) of all South African frog species ranges before and after 1996 regressed against the proportional change in range size for the same periods (R^2 = 0.02; $F_{(1,98)}$ = 2.4; p = 0.124). Negative values indicate southwards shifts in mean latitude.

There was also no relationship between range size change and longitudinal shifts ($R^2 = 0.02$; $p = 0.136$; Figure 14). However, the significant intercept (-13 038.3 m; $p < 0.001$) indicated mean westward range shifts of 13.0 km. Sixty-four species shifted westwards , while the remainder shifted eastward or remained stable.

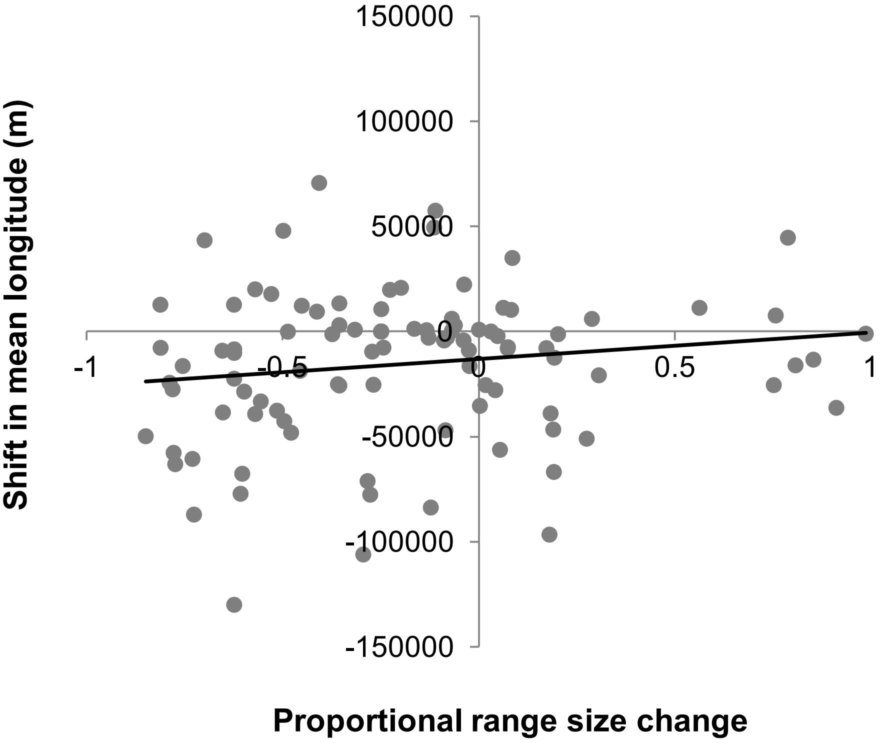


Figure 14: The shift in mean longitude (m) of all South African frog species ranges before and after 1996 regressed against the proportional change in range size for the same periods (R^2 = 0.02; $F_{(1,98)}$ = 2.3; p = 0.136). Negative values indicate westwards shifts in mean longitude.

There were significant shifts in the mean altitude of South African frog species ranges after 1996 (Figure 15). The mean upslope movement of species ranges of 47.6 m was significantly different from zero (p = 0.001). Upslope shifts were recorded for 61 species. Only 39 shifted downslope or remained stable. The relationship between these altitudinal shifts and range size change was not significant (R^2 = 0.03; p = 0.110).

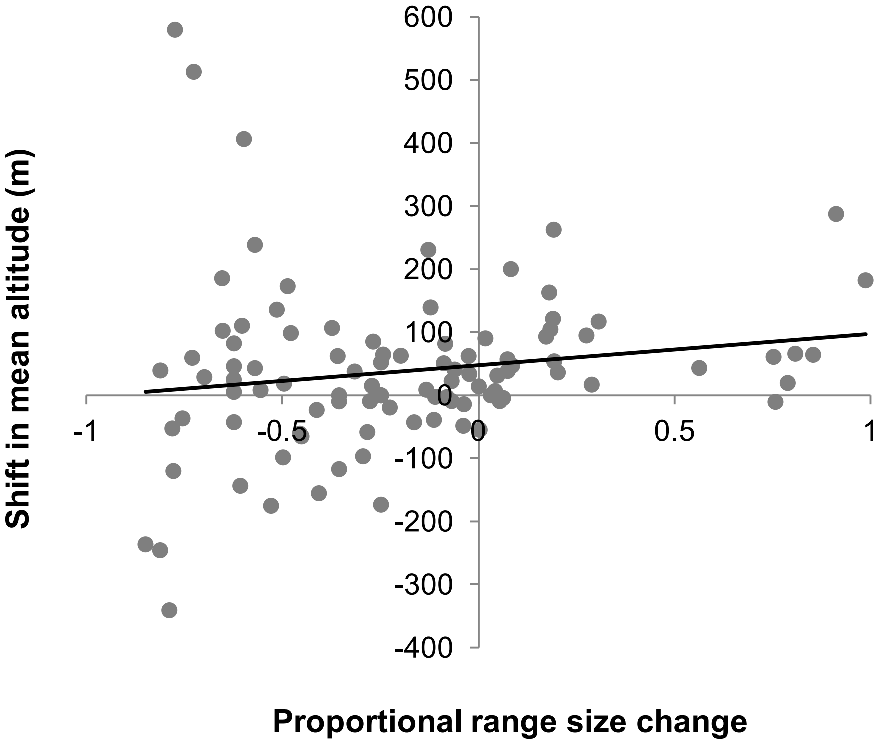


Figure 15: The shift in mean altitude (m) of all South African frog species ranges before and after 1996 regressed against the proportional change in range size for the same periods (R^2 = 0.03; $F_{(1,98)}$ = 2.6; p = 0.110). Negative values indicate a down-slope shift in mean altitude.

Fourteen species were indicators for the Bushveld biogeographic district (Alexander et al*.,* 2004), eleven (78.6%) of which shifted the mean centre of their ranges towards the northwest (Figure 16). On average, Bushveld species moved northwards by 19.7 km (p = 0.015) and westwards by 29.3 km (p = 0.014) regardless of changes to range size (Table 3). There was also a 74.9 m ($p < 0.001$) general upslope movement of mean range centres for this group, after a significant, positive relationship to range size change (R^2 = 0.47; p = 0.007) had been accounted for. Range contractions occurred in eight (57.1%) Bushveld species.

Table 3: Linear regressions between range size change and shifts in latitude, longitude and altitude for groups of species indicative of the biogeographic districts. Negative values indicate a southwards shift in latitude, westwards shift in longitude or a down-slope shift in altitude. (p < 0.05; ***p < 0.01).**

	R^2	Slope (m)	Intercept (m)
Bushveld District			
Mean latitude	0.06	-20994.8	19659.7**
Mean longitude	0.15	-53745.7	-29305.2**
Mean altitude	0.47***	195.1***	74.9***
Eastern Escarpment District			
Mean latitude	0.00	2262.5	-4226.3
Mean longitude	0.02	11106.2	-6177.2
Mean altitude	0.01	32.6	27.5
Winter/Transitional Rainfall District			
Mean latitude	0.15	-15229.8	25301.0**
Mean longitude	0.47**	37413.2**	-15670.3
Mean altitude	0.33	76.9	19.3

Of the 30 species indicative of the Eastern Escarpment District (Alexander et al., 2004; Figure 16), 19 (63.3%) had smaller recent ranges than historically. These species showed no significant trends in either latitudinal, longitudinal or altitudinal range shift (Table 3). There were also no significant relationships between range shift and range size change.

There was a northwards latitudinal shift for eight (88.9%) of the nine species indicative of the Winter Rainfall District (Alexander et al., 2004; Figure 16). This produced a significant mean northwards shift at range centres of 25.3 km ($p = 0.010$), that was unrelated to range size change ($R^2 = 0.15$; $p = 0.306$; Table 3). Longitudinal shifts were significantly related to range size change ($R^2 = 0.47$; $p = 0.041$), with contracting species more likely to shift westwards. Westward shifts independent of this relationship were not significant (-15 670.3 m; $p = 0.088$). There was no trend in mean altitude (19.3 m; $p = 0.423$).

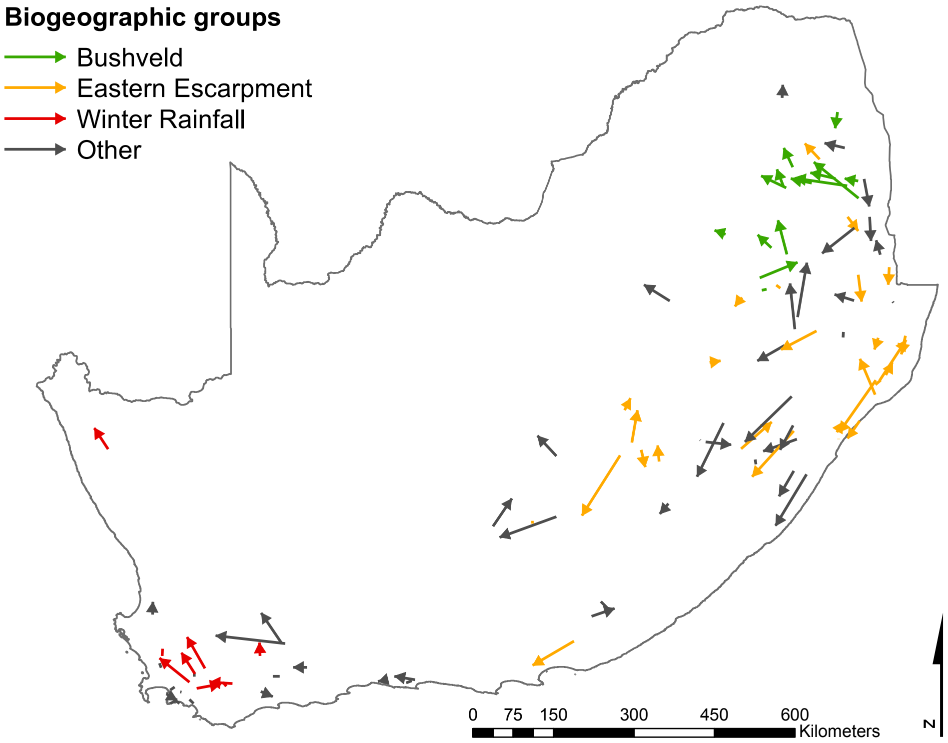


Figure 16: Map showing the shifts in mean range centre of all South African amphibian species. The lines indicate the distance moved by the mean centre of each species range before and after 1996 and the arrows show the direction. Coloured lines represent the species assigned to each biogeographic group: Bushveld = green; Eastern Escarpment = yellow; Winter Rainfall = red; Other species = grey.

4.4. Discussion

The majority of South African amphibian species have experienced contractions in overall range size (Botts et al., 2012). This is a serious finding, as 70% of the assessed species had suffered range contractions despite the increased sampling over time. If left uncorrected, the increased sampling intensity during the atlas sampling-period should have resulted in apparent range expansions (Botts et al., 2012). After the application of the correction factor, the reported range contractions are even more likely to indicate genuine reductions in range size. Fifty-three percent of the assessed species experienced severe range contractions. Globally, 42% of amphibian species are reported to be declining (IUCN et al., 2008). Although South African species have generally avoided the rapid population declines reported for other areas, they are still experiencing significant range contractions (Botts et al., 2012).

Land-cover changes that occur extensively across species ranges are expected to produce widespread range contractions, with negligible range shifts. Transformation of natural habitats in developing countries is ongoing, making it an important potential driver of range changes (Hockey et al., 2011). Land-cover changes have transformed much of South African land area, especially within the eastern and southern parts of the country (Fairbanks et al., 2000; see Figure 12c). The species included in the Eastern Escarpment District occur within this area of highly transformed land. Within their ranges, the port city of Durban is a core area of urban development along the coastline, and the Gauteng metropolitan area is responsible for extensive urban development in the northern regions. Sugarcane, plantations and other monoculture crops are widely cultivated in the eastern region (Fairbanks et al., 2000). A high proportion of Eastern Escarpment species showed range contractions (63.3%), but there were no significant range shifts. Land-cover change is thus a probable cause for the prevalent range contractions experienced by these species. This is an area of high amphibian richness, containing many more species than other biogeographic districts (Alexander et al., 2004). The coincidence of high species richness with high land-cover change has been noted for South African amphibians (Evans et al., 2006) as well as other taxa (Chown et al., 2003; Reddy & Dávalos, 2003; Evans et al., 2006). This situation is a recipe for systematic range contractions.

We found no evidence of the systematic poleward shifts predicted under a changing climate. Only 40% of species shifted southwards. The lack of comprehensive poleward range shifts may signify a differing response to climate change in southern hemisphere species or amphibians. Many of the documented range shifts from Europe and North America are from climate-sensitive high latitude regions. Much of the land area of the southern hemisphere and Africa is situated at lower latitudes, where species may show more moderate climate change responses, or a lagged effect (Parmesan et al., 1999; Root et al., 2003; Rosenzweig et al., 2007). Temperatures in the tropics, and even in the southern hemisphere temperate regions, have a weaker latitudinal temperature gradient than high-latitude northern areas (Wright et al., 2009). In these regions, species may follow the stronger altitudinal temperature gradients towards climate refuges (Wright et al., 2009). Additionally, erratic droughts and El Niño effects in the southern hemisphere complicate species responses to long-term climate change (Root et al., 2003; Simmons et al., 2004).

In the multiple taxon analysis by Hickling et al. (2006), the amphibian and reptile species were the only group to shift away from the poles. The widespread global amphibian declines suggest that amphibians are either more sensitive to environmental changes, or respond atypically, resulting in higher rates of population declines and higher Threat status than other taxa (Stuart et al., 2004). It is possible that amphibians are less able to achieve latitudinal range shifts. The inability of amphibians to disperse successfully to areas with newly suitable climate, or to persist in fragmented landscapes, may be the reason for contradictory range shifts (Warren et al., 2001; Araújo et al., 2006; Hickling et al., 2006). Altitudinal shifts necessarily involve shorter dispersal distances than latitudinal shifts, and South African amphibians showed observed upslope shifts. As well as having low mobility, amphibians are highly dependent on water availability (Carey & Alexander, 2003). Reproduction and aquatic life stages are dependent on the timing of rainfall events, the availability of standing water and the volume of runoff (McCarty, 2001; Carey & Alexander, 2003). Hence, precipitation may be a more important factor in amphibian range shifts than temperature. Thomas (2010) suggests that for tropical species, precipitation may be a more important range limiting factor than temperature. It has been shown that water availability (rather than latitude or high temperature seasonality) is the most important factor in determining amphibian range size in the Afrotropics (Whitton et al., 2011).

An average upslope shift of 47.6 m was recorded for all South African frog species as a whole. This upslope shift is greater than the vertical error for the elevation dataset (stated error 16 m, measured error 6 m, Rodríguez et al*.,* 2006), indicating a directional shift that is unrelated to data error. Differences in sampling intensity along an altitudinal gradient could have resulted in these observed upslope shifts. High altitude areas were acknowledged as being poorly sampled (Minter et al., 2004). However, poorly sampled high altitude cells were excluded from the analysis during sub-sampling. Thus, the effects of intensified sampling at higher altitudes were minimised as much as possible. Land-cover change is typically most extensive in low-lying areas (Midgley et al., 2003; Ellis & Ramankutty, 2008). Species will therefore experience the negative effects of land transformation as a loss of habitat from lowland areas of their ranges. We can therefore infer that localised extinctions may have occurred selectively at lower altitudes, resulting in an upslope shift. However, a concurrent range size reduction would be expected under this scenario. The relationship between range size changes and altitudinal shifts was not significant, indicating that the upward shifts are independent of range size changes. Climate change predictions forecast upslope shifts that are less likely to involve range contractions. Previous meta-comparisons of multiple species have recorded mean upslope shifts of 6.1 m (Parmesan & Yohe, 2003) or between 4.7 and 10.7 m per decade (Hickling et al., 2006). The 47.6 m upslope shifts documented for South African frogs were significant, with no relationship to range size change. Hence, hypothesised upslope shifts due to climate change are supported.

In South Africa, several scenarios may produce longitudinal shifts. A range expansion accompanied by a westward shift may signify a sampling effect, as sampling in the arid west has improved over time (see Figure 12a). Hockey et al. (2011) found that prevalent westward expansions in bird species were related to the increased artificial woodlands in the west, associated with spreading human habitats. An expansion of artificial wetlands in this region may have a similar effect for some frog species (Minter et al., 2004). Conversely, a westward shift and concurrent range contraction would suggest that the extensive land-cover changes in the east were responsible. The lack of westward shifts in Eastern Escarpment species does not support this hypothesis. Eastern Escarpment species are found in areas with highly transformed land, and although they experienced range contractions, there were no concurrent westward shifts. The westward range shifts recorded for all species had no relation to range size changes, and hence all of these scenarios are unlikely. The 13.0 km average westwards shift is small, occurring within the bounds of a single QDGC. A complex combination of these factors, or other unknown factors, must be acting to drive a significant, if short-distance, mean westward shift. Local westward shifts were also experienced by species of the Bushveld and Winter Rainfall Districts.

Species of the Bushveld District showed consistent mean range shifts in a northwesterly, upslope direction. Bushveld species occur predominantly in wooded landscapes in South Africa. The southern boundary of their distributions closely corresponds with the southern limit of subtropical woodlands (Alexander et al., 2004). None of these species are endemic to South Africa, but the mean centres of their South African ranges shifted significantly northwards by 19.7 km, westwards by 29.3 km and upslope by 74.9 m. Improved coverage of the western parts of these species ranges during the later sampling period may have resulted in an apparent westward shift. In this otherwise well-sampled region, precautionary sub-sampling ensured that sampling bias was limited.

Bushveld species mainly occupy two of South Africa's provinces, Limpopo to the northwest and Mpumalanga in the southeast. Land transformation in the southeastern Mpumalanga Province was higher as of 1994/1995, with 28.0% of the land transformed compared with only 16.5% in Limpopo (Fairbanks et al., 2000). Larger areas under cultivation in the east, and plantations restricted to the eastern escarpment, contributed to this difference (Fairbanks et al., 2000). In some parts of the eastern Bushveld region, a 39.7% increase in urban land-cover and 86.0% increase in formal cultivated lands have been recorded since 1993 (Coetzer et al*.,* 2010). These land-cover changes may have resulted in a decreased amphibian presence within the eastern part of species ranges, although there were no concurrent range size changes. The northwestern shift is also consistent with local climate change predictions for Bushveld species. The effects of local precipitation patterns and topographical heterogeneity predict an area of savanna biome resilience within the northwestern parts of these species ranges (see Figure 12d; Hannah et al*.,* 2002; Rouget et al., 2004). An increased density of frog presence within this area of Savanna Biome resilience could also explain the shifts of range to the northwest. The upslope shifts measured for Bushveld species also support the hypothesis of climate change as a driver.

The Winter/Transitional Rainfall District is found in areas that receive either winter rainfall or year round rainfall (Alexander et al., 2004). This region is associated with the Fynbos Biome. There is a high level of endemism for frogs, with all of the nine indicator species endemic to South Africa. Sampling was generally good, but several grid cells in the north and along the interior mountainous regions were only sampled during the later sampling period. These cells were excluded from the analysis, along with other poorly sampled grid cells. Most of these species (88.9%) shifted in a northwards direction, producing an average shift of 25.3 km northwards for this group. The oceanic boundary that these species experience to the west may have curtailed shifts westwards. Species that shifted west experienced range contractions, while expanding species shifted east.

In 1994/1995 the largest continuous section of cultivated land in the country was located along the southwestern coast, covering an area of 7 366 km^2 in low-lying areas below the Cape Fold Mountains (see Figure 12c; Fairbanks et al., 2000). The city of Cape Town, also on the west coast, transformed a further 50 km^2 (Fairbanks et al., 2000). The majority of Winter Rainfall species shifted their ranges in a northwesterly direction, toward these areas of high land-cover change. It is unlikely that the Winter Rainfall species would have benefitted from such extensive land transformations. Land-cover change, therefore, does not easily explain the observed range shifts.

Under future climate scenarios, the Fynbos Biome is expected to become further fragmented in the north and east, with biome resilience primarily occurring in the southwest (see Figure 12d; Hannah et al., 2002; Midgley et al., 2003). Shifts in the centres of several plant species ranges have been modelled, with predictions of mainly southeasterly shifts (Midgley et al*.,* 2003). Thus, the northwards shift in Winter Rainfall species also does not correspond well with available climate change predictions. However, MacKellar et al. (2007) showed that within the very northern parts of this region, rainfall had generally increased between 1950 and 1999, especially within low-lying coastal areas. Such changes in precipitation may be more important for amphibians that other aspects of climate change.

Sampling irregularities are one of the primary concerns when using historical and survey based species ranges to detect range dynamics (Donald & Fuller, 1998; Shaffer et al., 1998; Hickling et al., 2005; Hickling et al., 2006; Tingley & Beissinger, 2009). Incomplete sampling can cause uncertainties that impair the credibility of range change studies. Without a record of sampling effort, uneven geographic and temporal sampling is both unknown and intrinsic within the dataset. In the presence of unknown sampling biases, it is easy to attribute (correctly or incorrectly) any unexpected range shifts to sampling inaccuracy. Some of the range changes described here for South African amphibians are contrary to those predicted under global change scenarios. If sampling intensity differences had not been thoroughly accounted for, the default explanation for unexpected shifts might be that they are sampling related rather than a real phenomenon. However, the treatment of sampling bias issues in this investigation was comparable to that of previous climate change studies using grid-based species data (Hickling et al., 2005; Hickling et al., 2006). Range centres, as mean locations of all presence records, are more robust to sampling bias effects than range boundaries (Shoo et al., 2006). Significant shifts at mean range centres present the most convincing evidence of real range shifts. The concurrent assessment of range size change with range shifts also addressed sampling related effects.

Using this very conservative measure of range dynamics, we have shown significant range changes for South African amphibian fauna. In some instances, these range changes conform to global change predictions. The prevalent range contractions among species of the Eastern Escarpment are consistent with the high levels of transformed land within their ranges. Upslope shifts for all South African frogs suggest climate related shifts along an altitudinal temperature gradient. Species of the Bushveld District shifted upslope and northwest towards an area of Savanna Biome resilience to climate change. However, there are other cases where predicted range changes are not supported by the observed evidence. There were no systematic poleward shifts. Longitudinal shifts westward were unrelated to land-cover mediated contractions or expansions in range size. Winter Rainfall species shifted in a northwesterly direction against both land-cover and climate change predictions. This suggests that current predictions of range change responses to global change do not easily extend to southern hemisphere species, tropical species or amphibians. It is likely that these groups of species respond more to altitudinal and precipitation gradients, and that fragmented landscapes play a significant role in range changes.

4.5. References

Alexander, G. J., Harrison, J. A., Fairbanks, D. H. & Navarro, R. A. (2004) Biogeography of the Frogs of South Africa, Lesotho and Swaziland. In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H.H., Bishop, P. J. & Kloepfer, D. (eds) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

Araújo, M. B., Thuiller, W. & Pearson, R. G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33: 1712-1728.

Boakes, E. H., McGowan, P. J. K., Fuller, R. J., Chang-qing, D., Clark, N. E., O'Connor, K. & Mace, G. M. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8: e1000385.

Botts, E. A., Erasmus, B. F. N. & Alexander, G. J. (2011) Geographic sampling bias in the *South African Frog Atlas Project*: implications for conservation planning. *Biodiversity and Conservation* 20: 119-139.

Botts, E. A., Erasmus, B. F. N. & Alexander, G. J. (2012) Methods to detect species range size change from biological atlas data: a comparison using the *South African Frog Atlas Project*. *Biological Conservation* 146: 72-80.

Broennimann, O., Thuiller, W., Hughes, G. O., Midgley, G. F., Alkemade, J. M. R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12: 1079-1093.

Brown, J. H., Stevens, G. C. & Kaufman, D. M. (1996) The Geographic Range: Size, Shape, Boundaries and Internal Structure. *Annual Review of Ecology and Systematics* 27: 597-623.

Carey, C. & Alexander, M. A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9: 111-121.

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T. Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C. & Díaz, S. (2000) Consequences of changing biodiversity. Nature 405: 234-242.

Chown, S. L., Van Rensburg, B. J., Gaston, K. J., Rodrigues, A. S. L. & Van Jaarsveld, A. S. (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecological Applications* 13: 1233-1241.

Coetzer, K. L., Erasmus, B. F. N., Witkowski, E. T. F. & Bachoo, A. K. (2010) Land-cover change in the Kruger to Canyons Biosphere Reserve (1993 – 2006): A first step towards creating a conservation plan for the subregion. *South African Journal of Science* 106: 1-10.

Collins, J. P. & Storfer, A. (2003) Global amphibian declines: sorting the hypotheses. *Diversity and Distributions* 9: 89-98.

Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211-221.

CSIR & ARC (1996) South African National Land-Cover Database. CSIR Environmentek, Satellite Application Centre, Pretoria.

Cushman, S. A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.

Diniz-Filho, J. A. F., Bastos, R. P., Rangel, T. F. L. V. B., Bini, L. M., Carvalho, P. & Silva, R. J. (2005) Macroecological correlates and spatial patterns of anuran description dates in the Brazilian Cerrado. *Global Ecology and Biogeography* 14: 469-477.

Donald, P. F. & Fuller, R. J. (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study* 45: 129-145.

Ellis, E. C. & Ramankutty, N. (2008) Putting people on the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6: 439-447.

Erasmus, B. F. N., Van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. & Wessels, K. J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8: 679-693.

Evans, K. L., Van Rensburg, B. J., Gaston, K. J. & Chown, S. L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography* 15: 625-636.

Fairbanks, D. H. K., Thompson, M. W., Vink, D. E., Newby, T. S., Van den Berg, H. M. & Everard, D. A. (2000) The South African Land-cover Characteristics Database: a synopsis of the landscape. *South African Journal of Science* 96: 69-82.

Gaston, K. J. (2003) *The structure and dynamics of geographic ranges.* Oxford University Press.

Gardner, T. A., Barlow, J. & Peres, C. A. (2007) Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation* 138: 166-179.

Hannah, J., Midgley, G. F. Lovejoy, T., Bond, W. J., Bush, M., Lovett, J. C., Scott, D. & Woodward, F. I. (2002) Conservation of Biodiversity in a Changing Climate. *Conservation Biology* 16: 264-268.

Hickling, R., Roy, D. B., Hill, J. K. & Thomas, C. D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology* 11: 502-506.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.

Hockey, P. A. R., Sirami, C., Ridley, A. R., Midgley, G. F. & Babiker, H. A. (2011) Interrogating recent range change in South African birds: confounding signals from land use and climate change present a challenge for attribution. *Diversity and Distributions* 17: 254-261.

IUCN, Conservation International, and NatureServe (2008) An Analysis of Amphibians on the 2008 IUCN Red List.www.iucnredlist.org/amphibians. Cited 1 December 2011.

MacKellar, N. C., Hewitson, B. C. & Tadross, M. A. (2007) Namaqualand's climate: Recent historical changes and future scenarios. *Journal of Arid Environments* 70: 604-614.

McCarty, J. P. (2001) Ecological Consequences of Recent Climate Change. *Conservation Biology* 15: 320-331.

Midgley, G. F., Hannah, L., Millar, D., Thuiller, W. & Booth, A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation* 112: 87-97.

Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H., Bishop, P. J., Kloepfer ,D. eds. (2004) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington, DC.

Okes, N. C., Hockey, P. A. R. & Cumming, G. S. (2008) Habitat Use and Life History as Predictors of Bird Responses to Habitat Change. *Conservation Biology* 22: 151-162.

Parmesan ,C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Parmesan, C., Ryrhom, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kalla, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. S. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Pearson, R. G., Dawson, T. P. & Liu, C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography* 27: 285-298.

Pyke, G. H. & Ehrlich, P. R. (2010) Biological collection and ecological/environmental research: a review, some observations and a look to the future. *Biological Reviews* 85: 247-266.

Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography* 30: 1719-1727.

Reyers, B., Rouget, M., Jonas, Z., Cowling, R. M., Driver, A., Maze, K. & Desmet, P. (2007) Developing products for conservation decision making: lessons from a spatial biodiversity assessment for South Africa. *Diversity and Distributions* 13: 608-619.

Rich, T. C. G. & Woodruff, E. R. (1996) Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217-229.

Rodríguez, E., Morris, C. S. & Belz, J. E. (2006) A Global Assessment of the SRTM Performance. *Photogrammetric Engineering and Remote Sensing* 72: 249-260.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig ,C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.

Rosenzweig, C, Casassa, G., Karoly, D. J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root T. L., Seguin, B. & Tryjanowski, P. (2007) Assessment of observed changes and responses in natural and managed systems. In: Parry, M. L., Canziani, O. F., Palutikof, J. P. Van der Linden, P. J. & Hanson, C. E. (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, pp 79-131. Cambridge University Press, Cambridge, UK.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R. M., Mucina, L. & Rutherford, M. C. (2004) South African National Spatial Biodiversity Assessment 2004: Technical Report. Volume 1: Terrestrial Component. South African National Biodiversity Institute, Pretoria.

Shaffer, H. B., Fisher, R. N. & Davidson, C. (1998) The role of natural history collections in documenting species declines. *Trends in Ecology and Evolution* 13: 27-30.

Shoo, L. P., Williams, S. E. & Hero, J. M. (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology* 31: 22-29.

Sih, A., Jonsson, B. G. & Luikard G (2000) Habitat loss: ecological, evolutionary and genetic consequences. *Trends in Ecology and Evolution* 15: 132 -134.

Simmons, R.E., Barnard, P., Dean, W. R. J., Midgley, G. F., Thuiller, W. & Hughes, G. (2004) Climate change and birds: perspectives and prospects from southern Africa. *Ostrich* 74: 295-308.

Stearns, S. C. (1983) The influence of size and phylogeny on patterns of covariation among life history traits in mammals. *Oikos* 41: 173-187.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. *Science* 306: 1783-1786.

Thomas, C. D. (2010) Climate, climate change and range boundaries. *Diversity and Distributions* 16: 488-495.

Tingley, M. W. & Beissinger, S. R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution* 24: 625-633.

USGS (2004) Shuttle Radar Topography Mission, 3 ArcSecond scene. Global Land Cover Facility, University of Maryland.

Virkkala, R., Luoto, M., Heikkinen, R. K. & Leikola, N. (2005) Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *Journal of Biogeography* 32: 1957-1970.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J. M., Moss, D. & Thomas, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V. J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters* 8: 1138-1146.

Whitton, F. J. S., Purvis, A., Orme, C. D. L. & Olalla-Tárraga, M. Á. (2011) Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Global Ecology and Biogeography* 21: 179-190.

Wright, S. J., Muller-Landau, H. C. & Schipper, J. (2009) The Future of Tropical Species on a Warmer Planet. *Conservation Biology* 23: 1418-1426.

Chapter 5: Niche breadth

Botts, E. A., Erasmus, B. F. N. and Alexander, G. J. (in press) Small range size and narrow niche breadth predict range contractions in South African frogs. *Global Ecology and Biogeography*.

5.1. Introduction

In the context of amphibian declines, and global change, it has become evident that species are not equally vulnerable to population declines and extinction. Many studies have investigated the traits in amphibian species that confer higher susceptibility to declines (e.g. Murray & Hose, 2005; Bielby et al., 2008; Sodhi et al., 2008; Murray et al., 2011). The most consistently significant correlate with amphibian decline risk is geographic range size. Small-range species are more likely to decline, become threatened and eventually suffer extinction (Murray & Hose, 2005; Cooper et al., 2008; Sodhi et al., 2008; Devictor et al., 2010; Murray et al., 2011). This suggests that the attributes that give species small ranges may be important in predicting declines. Species with small ranges are often less abundant, less mobile, poorer competitors and have lower reproductive success than species inhabiting larger areas (Gaston, 1998; Kotze & O'Hara, 2003; Thuiller et al., 2005; Cooper et al., 2008; Sodhi et al., 2008).

A species will occupy an area based on three primary requirements: the environmental conditions must be suitable for the species to persist, the species must be able to disperse to the area and the species must successfully compete with other species and survive predation (Soberón, 2007; Hirzel & Le Lay, 2008; Olalla-Tárraga et al., 2011). Species with large ranges often tolerate a wide variety of conditions, while species with small ranges are only able to persist under a narrower range of conditions. Hence, the size of a species range is, at least partially, a spatial representation of its degree of specialisation (Kotze & O'Hara, 2003; Cooper et al., 2008; Sodhi et al., 2008; Devictor et al., 2010). At the large scales at which species range limits are usually defined, the suitability of environmental conditions is likely to be a relatively more important predictor of range size than biotic interactions (Pearson & Dawson, 2003; Soberón, 2007; Olalla-Tárraga et al., 2011).

Differing niche breadth distinguishes specialist from generalist species (Clavel et al., 2010). Specialists have narrow ecological niches and generalists broad niches, although a gradation exists between these two extremes (Kotze & O'Hara, 2003; Clavel et al., 2010). There are many ways to define species niches, but when assessing species distributions at broad scales, the realised

Grinnellian niche is the most appropriate definition (Soberón, 2007; Hirzel & Le Lay, 2008; Wiens et al., 2010; Olalla-Tárraga et al., 2011). Grinnell's definition of a species niche is based on the species response to the environmental conditions it experiences (Grinnell, 1917; Hirzel & Le Lay, 2008; Devictor et al., 2010). Hutchinson further developed this niche definition to include, simultaneously, the species response to multiple variables (Hutchinson, 1957; Hirzel & Le Lay, 2008; Devictor et al., 2010). The degree of specialisation occurs as an evolutionary trade-off between the variety of resources used and the efficiency of resource use (Clavel et al., 2010; Devictor et al., 2010). A species may be specialised along one ecological axis and a generalist in its tolerance of other conditions. Hence, different types of specialists exist: climate, habitat, diet and behavioural specialists (Williams et al., 2006; Devictor et al., 2010).

Since there are different types of specialist species, it follows that they will be vulnerable to different environmental changes. Climate specialists will be more sensitive to climate change than climate generalists, and habitat specialists more vulnerable to land transformation than habitat generalists (Broennimann et al., 2006; Murray et al., 2011). For a species to decline, it must be exposed to the decline drivers to which it is susceptible. Land-cover change is the biggest threat to amphibians (Stuart et al., 2004; Cushman, 2006; IUCN et al., 2008). Thus, declines among habitat specialists in highly transformed regions are likely to be prevalent. Climate change is also a global threat that may affect climate specialists in regions with large climate change anomalies (Thuiller et al., 2005; Broennimann et al., 2006). Predicting decline is therefore a twofold process of assessing the degree of specialisation of a species and comparing its range with the spatial pattern of decline drivers (Thuiller et al., 2005; Broennimann et al., 2006; Cooper et al., 2008; Murray et al., 2011). It is for this reason that single life history traits are often inconsistent in predicting decline across taxa and regions (Brook et al., 2008; Murray et al., 2011).

Large-scale empirical datasets can provide an effective measure of species realised niche breadth (Hirzel & Le Lay, 2008; Devictor et al., 2010). Most simply, this involves documenting the environmental conditions where species have been observed as present. This approach forms the basis for some types of species distribution modelling (Pearson & Dawson, 2003; Segurado & Araújo, 2004; Pearman et al., 2007; Hirzel & Le Lay, 2008). Multivariate statistics or models describe the relationship between species distributions and environmental data (Segurado & Araújo, 2004; Clavel et al., 2010; Devictor et al., 2010). Sampling intensity in biological atlases may not be high enough to capture the complete geographic ranges of species, and accuracy of niche breadth measurements will generally increase with improved sampling (Hortal et al., 2008). However, selecting an appropriate method to measure niche breadth from such a dataset will allow for consistent comparisons between species.

The *South African Frog Atlas Project* (*SAFAP*) is a comprehensive database of amphibian occurrence that provides an opportunity to measure the niche breadth of small-range species. South Africa's position at the continental edge means it has a high concentration of restricted range species (Whitton et al., 2011), which are possible specialists. The variation in climate, including tropical, temperate and arid conditions, and the nine biomes in the region are likely to produce a wide range in levels of specialisation. At least 68 (60.2%) species included in the *SAFAP* have undergone range contractions since 1996 (Botts et al. 2012). The aim of this study is to assess whether species specialisation on either habitat or climate axes has made South African amphibians more vulnerable to range contractions.

5.2. Methods

5.2.1. *The South African Frog Atlas Project*

The *South African Frog Atlas Project* (*SAFAP*) provided a comprehensive record of frog distributions in South Africa, Lesotho and Swaziland. It was compiled by combining historical amphibian records with a recent systematic survey. The approximately 16 900 historical records came primarily from natural history museums and dated from 1905 to 1995. The recent survey occurred between 1996 and 2003. It achieved a spatial coverage of 84% of the Quarter Degree Grid Cells (QDGCs) in the region and added circa 25 500 records to the *SAFAP* (Minter et al., 2004; Botts et al. 2012).

5.2.2. *Applying Ecological Niche Factor Analysis to measure niche breadth*

The *SAFAP* species distribution data formed the basis of the niche breadth calculation. As it is a presence-only dataset, the most appropriate measure of multidimensional niche breadth was an Ecological Niche Factor Analysis (ENFA) (Hirzel et al., 2002; Segurado & Araújo, 2004; Basille et al., 2008). ENFA is a multivariate statistical method that combines many variables into several uncorrelated factors (Segurado & Araújo, 2004). This method extracts two or more factors that describe a species niche: a marginality factor that expresses niche position relative to the study area and specialisation factors that describe niche breadth (Hirzel et al., 2002; Segurado & Araújo, 2004; Basille et al., 2008). ENFA is available as part of the BIOMAPPER software (Hirzel et al., 2007).

Niche properties that are conserved over time are more likely to be involved in range contractions. When niche properties remain constant, species must track suitable conditions or suffer from population declines (Hirzel & Le Lay, 2008; Wiens et al., 2010). To ensure that niche conservatism was a valid assumption, we included only abiotic variables, and retained the coarse resolution and large spatial extent of the *SAFAP* (Pearson & Dawson, 2003; Pearman et al., 2007; Wiens et al., 2010). The *SAFAP* species distribution data have a QDGC resolution (approximately 25 x 25 km) and an extent of approximately 1 600 km across the widest latitude of South Africa. Appropriate variables at this scale are those related to climate (acting at spatial extents >200 km), topography (1 – 2 000 km) and land-use (<200 km) (Pearson & Dawson, 2003). The variables were thus grouped into climate and land-cover themes (Hirzel & Le Lay, 2008) to separate effects at different scales and to discover differences between habitat and climate specialisation. For amphibians, which are ectothermic and generally require water for breeding stages, variables related to temperature and water availability are predicted to have a physiological effect that may be important in limiting their ranges (Olalla-Tárraga et al., 2011).

Climate variables were acquired from the *South African Atlas of Climatology and Agrohydrology* (Schulze, 2007) and re-sampled to a QDGC resolution. The summary climate variables included in the analysis were mean annual temperature, mean annual precipitation, mean annual potential evaporation and mean annual humidity. Precipitation seasonality was also included, as it is an aspect of climate variation that may limit amphibian ranges (Bielby et al. 2008; Sodhi et al., 2008; Whitton et al., 2011). We used the coefficient of variation of median monthly rainfall as a measure of precipitation seasonality. This is the intra-annual variability in rainfall, indicating whether rain falls throughout the year or only during a short rainy season. Precipitation in the driest month and mean minimum temperature in the coldest month were used to incorporate extreme climates (Whitton et al., 2011) to which amphibians are commonly averse. Temperatures can co-vary locally with changes in altitude, so mean altitude was included with the climate variables. Altitude was available as a 90 m resolution digital elevation model from the Shuttle Radar Topography Mission (USGS, 2004).

The National Land Cover Database (CSIR & ARC, 1996) provided the percentage coverage per QDGC of cultivated, degraded, forest and woodlands, grassland, thicket and bushland and urban land types (Fairbanks et al., 2000). The coverage of wetlands was calculated from the National Wetlands Inventory (SANBI, 2010). A rivers dataset (RQS, 2010) was used to calculate the mean distance to any river within each QDGC. Standard deviation of altitude was used to provide an estimate of topographical heterogeneity. Although these data were compiled at different scales, they were all intended for use at a national extent. By re-sampling them to the large QDGC resolution, we have minimised any inconsistencies between them.

ENFA fails if the observation-to-variable ratio is too small. Species with smaller range size could only be included if the number of variables was kept to a minimum. Thus, the ENFA required a balance between including as many variables as possible to achieve meaningful niche breadth measures and reducing the overall number of variables. Eight climate variables and nine habitat variables were selected for the ENFA, and were retained for all species to ensure comparability. Still, the ENFA did not proceed successfully for many of the smaller range species and we thus excluded all species with eigenvalues larger than 1 000 for either the habitat or climate analysis. The 41 species that were excluded had range sizes smaller than 55 QDGCs and all but six of these species had experienced range contractions. Only 66 species had reliable ENFA results for both climate and habitat. Hence, all investigations were restricted to these 66 species, or to the 23 species among them that were endemic to the study area.

ENFA may be biased if the underlying species presence data are biased (Hirzel et al., 2002). Thus, the sampling quality of the *SAFAP* determined the accuracy of the ENFA niche breadth measures. We conducted an ENFA on all the sampled grid cells to give an indication of how thoroughly the chosen variables were represented within the sampled portion of the study area. A sampling probability map was created using the number of factors recommended by the broken-stick advice included with BIOMAPPER. To evaluate the quality of sampling for each species within its most inclusive possible range, we calculated the mean sampling probability for each species using the amphibian distribution polygons available from the Global Amphibian Assessment (IUCN, 2009). This mean sampling probability per species was then used to weight the analyses, such that species with ranges in poorly sampled areas, which are also likely to have incomplete niche breath measurements, were given lower weight.

5.2.3. *Relating niche breadth to range size change*

Range size change was related to measures of species specialisation using linear regressions (Broennimann et al., 2006). An overall specialisation factor per species is a product of the ENFA (Hirzel et al., 2002). Its inverse, Tolerance, has a more normal distribution and is easier to interpret, varying from zero (a highly specialised species) to one (a highly generalised species). Thus, Tolerance was used in the linear regressions as a predictor of range size change. A separate regression was performed for the endemic species. These are the only species whose entire range, and thus complete niche, is included in the study area. All regressions were repeated with each species weighted according to its sampling probability. Stepwise multiple linear regressions were also performed that included range size (log), habitat tolerance and climate tolerance to discover the relative importance of these variables in predicting range size change, for all species and endemic species.

Measures of range size change can also be affected by sampling biases, particularly changes in sampling over time. After comparing a number of different approaches on hypothetical ranges with known change, we identified the correction factor of Rich & Woodruff (1996) as the best method to correct for differing sampling intensities between the two sampling periods (Botts et al., 2012). This method applies the correction $R = CA + (1 - C).(A^2/n)$ (where C is a constant correction factor, A is the historical measured range size of each species and n is the total number of grid cells sampled) to better equate the historical range sizes with the higher sampling of the atlas period. After the correction, range size change was measured as the proportional difference between the number of grid cells occupied by each species in the historical and atlas sampling periods. For the 66 species included in the analysis, the average historical median year in which they were recorded was 1973 ± 7. The difference between the historical and atlas median years per species was 27 ± 7 years on average, and longer than 11 years for all species. We regard this gap as long enough for genuine range size changes to be readily observed. Since there was no significant relationship between the length of the gap and range size change ($R^2 = 0.009$; $F_{(1,64)} = 0.58$; $p = 0.45$), it was not considered a factor in any further analyses.

Ecological similarities among related species may result in non-independence of data points during comparisons (Cooper et al., 2008; Olalla-Tárraga et al., 2011). To discover any phylogenetic dependence among data points, we performed nested ANOVAs for all variables included in the regressions. This method is appropriate when there is no available phylogeny for the taxon, and Family and Genus (nested within Family) are used as taxonomic substitutes for phylogeny (Stearns, 1983; Cooper et al., 2008). Since none of the ANOVAs showed a significant result (Range size change: $F = 1.01$; $p = 0.4794$; Climate tolerance: $F = 1.03$; $p = 0.4505$; Habitat tolerance: $F = 0.98$; $p = 0.5045$), the assumption of independence for the regressions was considered to have been met.

5.2.4. *Investigating the spatial concurrence between habitat specialists and land transformation*

Habitat specialists with range contractions are expected to be located in regions with high land transformation. We mapped the spatial distribution of contracting habitat specialists. To map land transformation in South Africa, we used the summed land-cover classes urban, cultivated and degraded from the National Land Cover database (CSIR & ARC, 1996). From these data, we calculated the percentage of transformed land per QDGC within the distributional area of contracting habitat specialists. Unfortunately, no such observed climate change data were available for the region, and hence the corresponding climate change analysis could not be conducted.

5.3. Results

Total recorded range size of species was a significant, positive predictor of range size change (Figure 17). Species with smaller ranges were more likely to have experienced range contractions. Large-range species were more likely to have expanded in range size. For all 66 species that were included in the analyses, total range size explained 35% of the variation in range size change ($R^2 = 0.35$; $F_{(1,64)} = 34.58$; $p < 0.0001$). Restricting the analysis to only the 23 endemic species increased the strength of this relationship to 39% ($R^2 = 0.39$; $F_{(1,21)} = 13.46$; $p = 0.0014$), and also increased the slope (Figure 17).

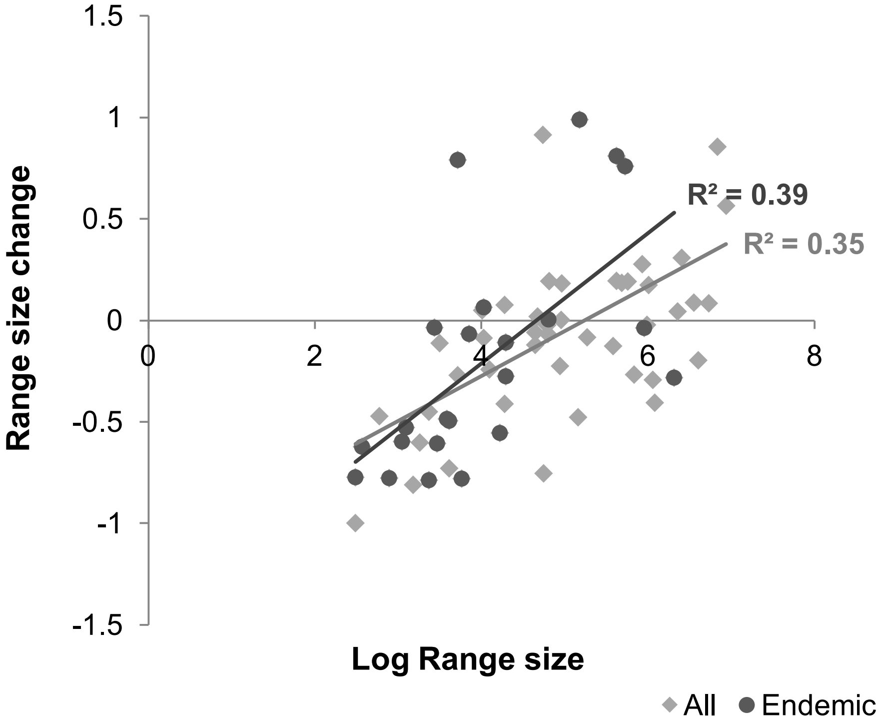


Figure 17: The effect of total range size (log number of grid cells) on the change in range size (proportional change in number of grid cells between the historical and recent sampling, after the Rich and Woodruff (1996) correction). The pale grey diamonds and pale grey regression line represent all 66 species. The dark grey circles and dark grey regression line represent the 23 endemic species.

We tested the quality of sampling by running an ENFA for all sampled cells. If all the grid cells in the study area had been sampled, we would expect a marginality score of 0 and a tolerance score of 1. However, the representativeness of the sampled cells for the chosen variables depends on which cells where sampled. For climate variables, the marginality score was 0.16 and tolerance 0.99. For the habitat variables, the marginality score was 0.14 and tolerance 0.97. This indicates that sampling of the study area was comprehensive, but not complete. The variables contributing most to the marginality scores give an indication of sampling biases. Sampling probability was higher in areas with high cultivation cover (0.58), high altitudinal variation (0.50), high mean annual rainfall (0.48), high mean annual humidity (0.47), high precipitation in the driest month (0.34), high urban cover (0.32) and high precipitation seasonality (0.31). Sampling was low in regions with high annual evaporation (-0.51) that are far from rivers (-0.41).

Applying ENFA to each species provided an estimation of climate and habitat specialisation for all species. The variables grassland cover, altitudinal variation and thicket/bushland cover contributed most to habitat specialisation with mean specialisation factor values across species of 0.52, 0.32 and 0.31 respectively. For climate variables, the highest mean specialisation factor contributions were for precipitation seasonality (0.41), precipitation in the driest month (0.33) and mean altitude (0.31).

More species showed climate specialisation than habitat specialisation (Figure 18). Forty-nine species had climate tolerance values below 0.5. Conversely, only 11 species had habitat tolerance values below 0.5. However, according to a Spearman rank correlation, most habitat specialists were also climate specialists ($\rho = 0.82$; $p < 0.0001$).

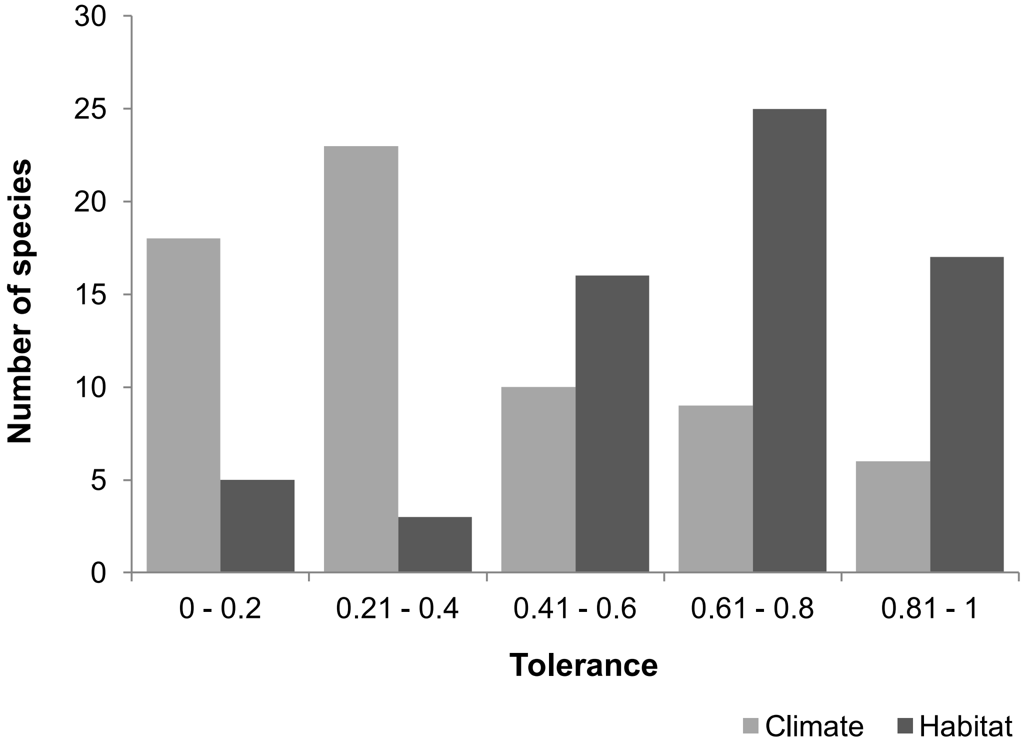
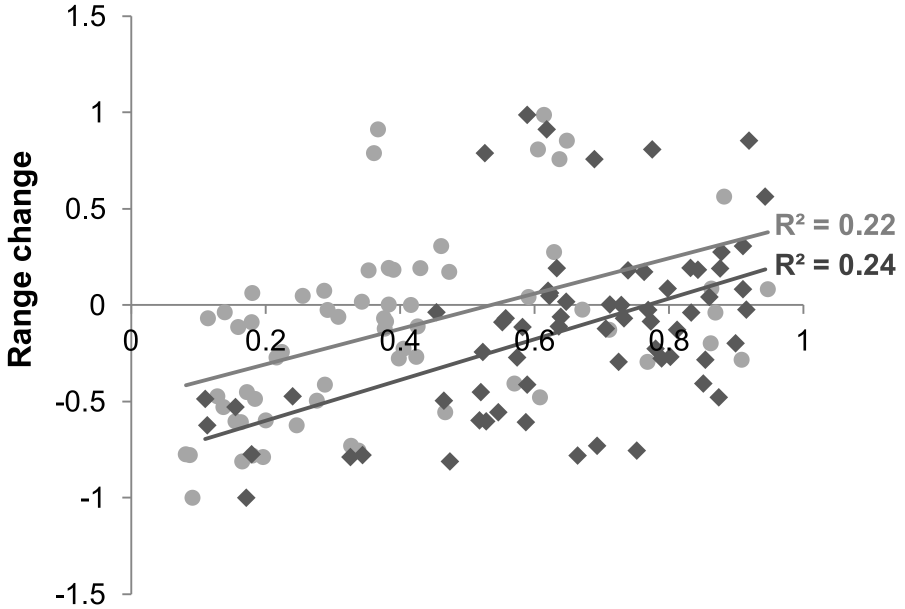


Figure 18: The frequency distribution of species for climate and habitat tolerance. Tolerance is the inverse of specialisation, a product of the ENFA analysis. Values close to one indicate generalist species and values close to zero indicate specialist species.

Both climate niche breadth and habitat niche breadth were positively related to range size change. Species with low tolerance (highly specialised) in either climate or habitat were more likely to have experienced range contractions (Figure 19a). Habitat tolerance ($R^2 = 0.24$; $F_{(1,64)} = 20.43$; $p < 0.0001$) had a slightly stronger relationship with range size change than did climate tolerance ($R^2 = 0.22$; $F_{(1,64)} = 17.65$; $p < 0.0001$). Weighting the regression with a relative measure of sampling probability for each species slightly reduced the strength of both regressions. After weighting, habitat tolerance explained 22% of the variation in range size ($F_{(1,64)} = 18.54$; $p < 0.0001$) and climate tolerance 20% ($F_{(1,64)} = 15.65$; $p = 0.0002$).

Restricting the regressions to only endemic species showed that climate niche breadth ($R^2 = 0.28$; $F_{(1,21)} = 8.23$; $p = 0.0092$) was now a better predictor of range size changes than habitat niche breadth ($R^2 = 0.22$; $F_{(1,21)} = 5.93$; $p = 0.0239$; Figure 19b). Again, weighting the regression with sampling probability slightly decreased the strength of the relationships: climate niche breadth explained 24% ($F_{(1,21)} = 6.48$; $p = 0.0188$) of the variation in range size change, and habitat niche breadth 21% ($F_{(1,21)} = 5.43$; $p = 0.0299$).

a. All species



b. Endemic species

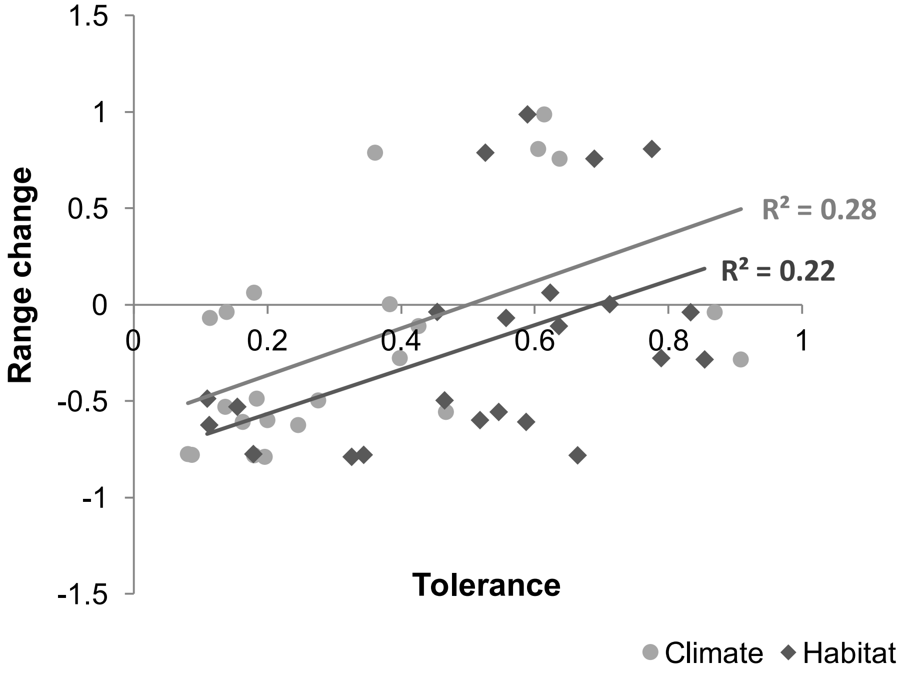


Figure 19: The effect of tolerance on range size changes for (a.) all 66 species and (b.) the 23 endemic species. The dark grey diamonds and dark grey regression lines represent habitat tolerance. The pale grey circles and pale grey regression lines represent climate tolerance.

Multiple linear regression confirmed the results of the individual regressions. The high correlation between range size (log), habitat tolerance and climate tolerance meant that only one of these variables was generally retained after a stepwise selection procedure. When range size was included in the model, it was always the only variable that was retained (Table 4). Excluding range size, only habitat tolerance remained in a stepwise regression of all species, and only climate tolerance remained for endemic species (Table 4).

Table 4: The results of multiple linear regressions including the variables range size (log), habitat tolerance and climate tolerance to predict range size change. The last two regressions excluded the variable range size (log). Only the F-values and significance of variables remaining after a stepwise selection procedure are shown in the table. (*p < 0.001; **p < 0.05)**

	Range size (log)	**Habitat tolerance**	**Climate tolerance**	**Model R^2**
Including range size, all species	34.58***			0.35***
Including range size, endemic species	13.46**			0.39**
Excluding range size, all species		20.43***		0.24***
Excluding range size, endemic species			8.23**	0.28**

Eleven species had overall habitat tolerance lower than 0.5, indicating that they are specialists. Contracting habitat specialists were concentrated along the eastern and southwestern coastlines and escarpments (Figure 20). The mean tolerance of the 11 contracting specialist species was 0.28, and their ranges had contracted proportionally by an average of -0.62. According to the mean ENFA specialisation factor results, these species were most likely to be specialised in their use of grassland (0.43), thicket and bushland (0.41) and altitudinal variation (0.31) habitat factors. Contracting habitat specialists were found in regions with a significantly higher ($t = -7.45$, $p < 0.0001$) mean percentage of transformed land per grid cell (33.69%) than the national average (20.62%). There were no expanding habitat specialists with which to compare this result.

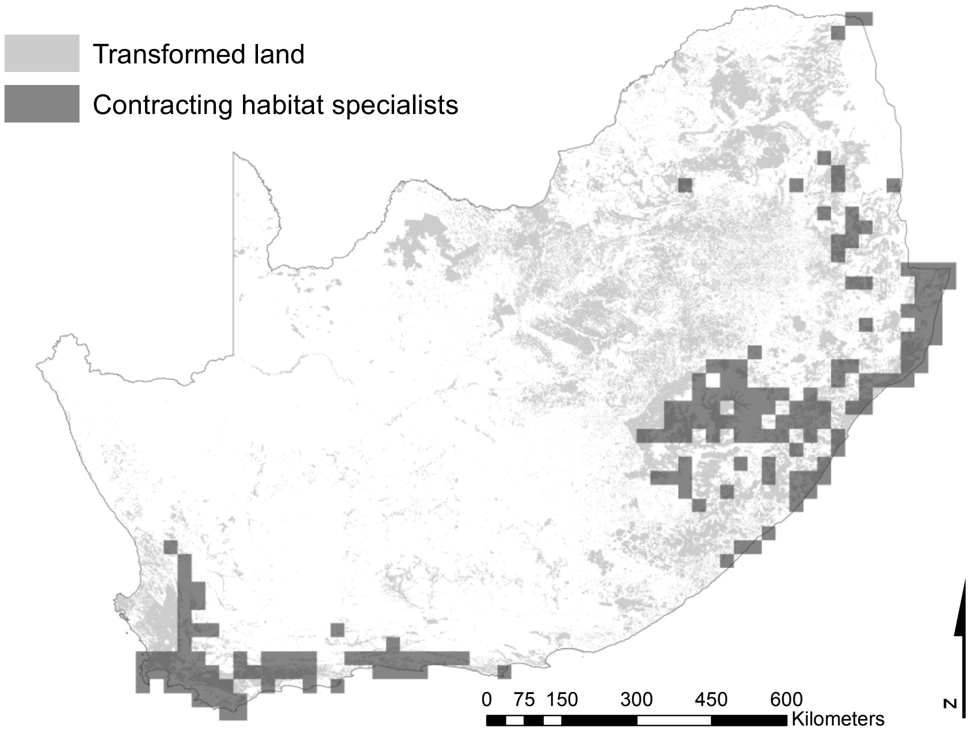


Figure 20: The spatial distribution of contracting habitat specialists within the study area (dark grey grid cells). Transformed land is shown in pale grey as a base layer (National Land Cover; CSIR & ARC, 1996).

5.4. Discussion

Total range size explained 39% of the variation in range size change for endemic South African frogs. Species with small ranges were more likely to have suffered range contractions than were species with large ranges. This is consistent with both global and regional findings for amphibians. Globally, range size has been shown to explain between 45% (generalised linear mixed effects model; Sodhi et al., 2008) and 50% (linear regression; Cooper et al., 2008) of the variation in threat risk. Among only endemic Australian amphibians, range size explained 20% of the variation in decline risk (linear regression; Murray & Hose, 2005). Differences in resolution and extent of these studies may contribute to the differences in explanatory value. The large extent of global scale analyses probably contributed to their higher predictive value than the regional scale studies (Cooper et al., 2008). Only global scale analyses are able to include the widest ranging species, the inclusion of which amplifies the correlation between range size and decline. The regional studies differed in resolution. South African frog data was assembled at a quarter-degree grid resolution, while the Australian data used a half-degree grid resolution. The higher predictive value in our study implies that the relationship between range size and range size change is better observed at finer resolutions. From the consensus among these studies, it becomes clear that small range sizes either cause or facilitate population declines in amphibians. Narrow niche breadth may be one factor that contributes to declines in small-range species.

The *SAFAP* proved to be an adequate database with which to measure species niche breadth. The marginality factors for the sampled area highlighted some of the similar sampling biases that were known from previous analyses (Minter et al., 2004; Botts et al., 2011). Sampling probability was higher in areas with high human habitation (cultivation, urban) and high moisture (rainfall, humidity). Sampling was poorer in arid areas (far from rivers with high evaporation). However, overall marginality and specialisation factors for the sampled area were very near to the maximum values for the entire study area. This indicates that, despite the sampling biases, the *SAFAP* is an unexpectedly complete sample of the possible conditions that species may experience within the study area. Weighting the results with a measure of sampling probability also had little effect on the essential findings of the regressions. Unfortunately, many of the species with the smallest ranges could not be included in the analysis. ENFA fails if the sample sizes are few in comparison to the number of variables. Low sample sizes were associated with species presence in few grid cells. Almost all of the small-range species that were excluded showed range contractions. Hence, the exclusion of these species is likely to have reduced the significance of the results.

South African frogs were more likely to have narrow climate niches than narrow habitat niches. This finding emphasises the importance of scale in defining species range limits. Species presence at the coarse resolution of the *SAFAP* is more likely to be associated with variation in climate than habitat. Climate is the dominant factor in determining species range limits at larger scales (Pearson & Dawson, 2003; Broennimann et al., 2006). Although particular microhabitat conditions (especially the accessibility of water) are important for amphibians at smaller scales, these variables can be only poorly represented at larger scales. Macrohabitat variables are at best summaries of the coverage or density of the microhabitat features relevant to species (Soberón, 2007). The coarse resolution means that many different microhabitats are present in a single grid cell, whereas the climate of a grid cell is more homogenous. Thus, climate factors would probably be superior to habitat variables in modelling species distributions at this resolution. However, both climate and habitat variables proved valuable in defining and understanding the ecological niches of South African species.

Certain macrohabitat variables were useful in describing amphibian specialisation. In particular, habitat specialists were concentrated in two biomes. Grassland specialists occurred mostly in the moist coastal and montane grasslands along the eastern coast. Fynbos specialists occurred in the equivalent coastal and montane Fynbos vegetation on the western coast. These two regions also correspond to areas of high endemism. The Maputaland-Pondoland-Albany centre of endemism on the eastern coast of southern Africa has been shown to accommodate high numbers of endemics from a wide variety of taxa, including amphibians (Perera et al., 2011). The Western Cape is well known for its endemic plants (Goldblatt & Manning, 2002), but it also contains many endemic amphibians (Alexander et al., 2004). Specialist species were concentrated in grid cells with high altitudinal variation. This supports the hypothesis that these centres of endemism were established in areas of physical heterogeneity that supported refuges from historical climate change (Alexander et al., 2004). It would appear that the spatial distribution and history of small ranges, endemism and habitat specialisation are all interrelated. The few species that were habitat specialists all had small ranges.

Many more species were classified as climate specialists than habitat specialists, including species with larger range sizes. Climate specialists were almost exclusively defined by variables relating to the timing of precipitation: precipitation seasonality and precipitation in the driest month. Some of the climate specialists were found in regions where precipitation is highly seasonal. In these situations, most rain falls during a short period and there is little rainfall during the driest month. This rainfall pattern dominates in the northeastern part of South Africa and reflects the tropical savanna climate that extends into South Africa from the tropics of Africa. Such species are also likely to be non-endemics, with ranges extending into similar conditions outside of the study area. Alternatively, other climate specialists were found in areas where precipitation seasonality is low, and moderate rain falls even in the driest month of the year. These climate conditions occur along the southern coastline of South Africa, and species inhabiting this region are more likely to be endemics.

Both habitat and climate specialisation resulted in species having a higher risk of range contraction. Niche breadth explained between 20 and 28% of the variation in range size change. Species with narrower niches were more likely to have undergone range contractions, and species with broad niches were more likely to have expanded. Species with narrow niches can only tolerate a narrow range of conditions within which they are able to survive and reproduce. In South Africa, specialist species occurred in particular biomes or precipitation zones. Outside of these conditions, individuals of these species will have reduced survival. Any disturbance in their favoured conditions will likewise result in population declines. While niche breadth is not as good a predictor of range contractions as range size, it has the advantage of providing additional information about species preferences and can thus highlight possible agents of decline.

Habitat specialisation was a better predictor of range size change for all species, while climate specialisation was a better predictor for endemic species. This highlights some of the differences between habitat and climate specialisation, as well as between endemic and non-endemic species. All habitat specialists, whether endemic or not, experienced range contractions. When all species were considered, many species of habitat generalists expanded their ranges. However, among endemic species there were fewer expanding habitat generalists. Thus, habitat specialisation lost some predictive value when non-endemic, expanding habitat generalists were excluded. Alternatively, not all climate specialists experienced range contractions. Many of the expanding species among non-endemics were climate specialists. These non-endemic climate specialists are generally wide ranging species that are limited within South Africa to the highly seasonal tropical savanna climate in the northeast. Climate specialisation was a better predictor of range size change when these non-endemic, expanding climate specialists were removed. In both cases, non-endemic species that had expanding ranges in South Africa influenced the ability of niche breadth to predict range size changes.

While both range size and niche breadth were significant predictors of range size change, the moderate R-square values indicate that other factors probably also play a part in declines. The small population paradigm states that for species with very few individuals, genetics and demographics within small populations may directly cause declines (Caughley, 1994). For most species, however, the declining population paradigm is more relevant (Caughley, 1994). Intrinsic species characteristics can only predispose a species to decline, making it more susceptible to the effects of extrinsic environmental agents (Caughley, 1994; Murray et al., 2011). A combination of intrinsic characteristics such as fecundity, reproductive strategy, body size, physiology and mobility may determine a species degree of susceptibility to decline (Kotze & O'Hara, 2003; Murray & Hose, 2005; Thuiller et al., 2005; Broennimann et al., 2006; Bielby et al., 2008; Cooper et al., 2008; Okes et al., 2008; Sodhi et al., 2008; Murray et al., 2011). In many of the relevant studies, small range size is the most significant single life history trait involved in threat or decline risk for amphibians (Murray & Hose, 2005; Cooper et al., 2008; Sodhi et al., 2008). Our analysis showed that narrow niche breadth was also a significant factor in range contractions. It is probable that narrow niche breadth is a major basis for small ranges at large scales (Soberón, 2007; Hirzel & Le Lay, 2008; Devictor et al., 2010; Pearson & Dawson, 2003). Thus, range size, and to a lesser extent niche breadth, are likely to be the best intrinsic characteristics for a-priori prediction of declines. However, a proximate cause is necessary to instigate declines (Caughley, 1994). The proximate cause is usually a direct change in the environment (Caughley, 1994; Murray et al., 2011). Thus, a combination of the degree of intrinsic susceptibility and the extent of external threats will ultimately determine the magnitude of range changes (Murray et al., 2011).

Multiple species and spatial factors contributed collectively towards range contractions for South Africa amphibians. Small-range species were shown to be more vulnerable to range contractions. These small-range species are also habitat specialists. While successful within their preferred environment, habitat specialists will generally adapt poorly to conditions of land-cover change (Clavel et al., 2010; Devictor et al., 2010; Murray et al., 2011). Small-range specialists were also grouped within areas of high endemism. Since endemics are limited to the study area, declines among these species convey a significant likelihood of globally important biodiversity loss. The concentration of endemic, small-range specialists within certain biomes means that any threat in these areas will affect many species. Finally, the biomes and associated vegetation types that contain these susceptible species are also the most transformed regions of the study area (Fairbanks et al., 2000; Reyers et al., 2001). The accrual of these multiple threats towards small-range species may represent an unfortunate coincidence. However, the historical processes responsible for the current biogeographic patterns of species distribution suggest that a similar concentration of events may be found for other regions, taxa or variables (Broennimann et al., 2006; Murray et al., 2011).

Our study provides corroborating evidence for the susceptibility of small-range, specialist species to range contractions and declines. The extirpation of small-range specialist species from an area may not only contribute to biodiversity loss, but may influence the stability and functioning of the ecosystem (Clavel et al., 2010). Hence, small-range specialists are an important target for conservation action. Furthermore, conserving vulnerable ecosystems may ensure the protection of more than one vulnerable species. Setting high conservation priority for areas of endemism will incorporate the ranges of many small-range, specialist species. Since climate specialisation was an even better predictor of range contractions among endemic species than habitat specialisation, further investigation of the spatial congruence between climate specialists and climate anomalies (Thuiller et al., 2005; Broennimann et al., 2006) is necessary.

5.5. References

Alexander, G. J., Harrison, J. A., Fairbanks, D. H. & Navarro, R. A. (2004) Biogeography of the Frogs of South Africa, Lesotho and Swaziland. In: Minter, L. R., Burger, M., Harrison, J. A., Braack, H.H., Bishop, P. J.

& Kloepfer, D. (eds) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington DC.

Basille, M., Calange, C., Marboutin, E., Anderson, R. & Gaillard, J.- M. (2008) Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. *Ecological Modelling* 211: 233-240.

Bielby, J., Cooper, N., Cunningham, A. A., Garner, T. W. J. & Purvis, A. (2008) Predicting susceptibility to future declines in the world's frogs. *Conservation Letters* 1: 82-90.

Botts E. A., Erasmus B. F. N. & Alexander G. J. (2011) Geographic sampling bias in the *South African Frog Atlas Project*: implications for conservation planning. *Biodiversity and Conservation* 20: 119-139.

Botts, E. A., Erasmus, B. F. N. and Alexander, G. J. (2012) Methods to detect species range size change from biological atlas data: a comparison using the *South African Frog Atlas Project. Biological Conservation.* doi:10.1016/j.biocon.2011.10.035.

Broennimann O., Thuiller W., Hughes G. O., Midgley G. F., Alkemade J. M. R. & Guisan A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12: 1079-1093.

Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23: 453-460.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology* 63: 215-244.

Clavel, J., Julliard, R. & Devictor, V. (2010) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* 9: 222-228.

Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211-221.

CSIR & ARC (1996) South African National Land-Cover Database. CSIR Environmentek, Satellite Application Centre, Pretoria.

Cushman S. A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology* 47: 15-25.

Fairbanks, D. H. K., Thompson, M. W., Vink, D. E., Newby, T. S., Van den Berg, H. M. & Everard, D. A. (2000) The South African Land-cover Characteristics Database: a synopsis of the landscape. *South African Journal of Science* 96: 69-82.

Gaston, K. J. (1998) Rarity as double jeopardy. *Nature* 394, 229-230

Goldblatt, P. & Manning, J.C. (2002) Plant diversity of the Cape Region of southern Africa. *Annals of the Missouri Botanical Gardens,* 89, 280-302.

Grinnell, J. (1917) The Niche-Relationships of the California Thrasher. *The Auk* 34: 427-433.

Hirzel, A. H. & Le Lay, G. (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45: 1372-1381.

Hirzel, A. H., Hausser, J. & Perrin, N. (2007) Biomapper 4.0. Laboratory for Conservation Biology, Department of Ecology and Evolution, University of Lausanne, Switzerland. http://www2.unil.ch/biomapper. 24 October 2011

Hirzel, A. H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology* 83, 2027-2036.

Hortal, J., Jiménez-Valverde, A., Gómez, J. F., Lobo, J. M. & Baselga, A. (2008) Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* 117: 847-858.

Hutchinson, G. E. (1957) Concluding Remarks. Population Studies: Animal Ecology and Demography. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415-427

IUCN (2009) IUCN Red List of Threatened Species. Version 2009.1. http://www.iucnredlist.org. Cited 15 June 2009.

IUCN, Conservation International and NatureServe (2008) 2008 IUCN Red List www.iucnredlist.org/amphibians. Cited 18 October 2010.

Kotze D. J. & O'Hara R. B. (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135: 138-148.

Minter, L. R., Burger, M., Harrison, J. A., Braack, H. H., Bishop, P. J., Kloepfer ,D. eds. (2004) *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland.* SI/MAB Series #9. Smithsonian Institution, Washington, DC.

Murray, B. R. & Hose, G. C. (2005) Life-history and ecological correlates or decline and extinction in the endemic Australian frog fauna. *Austral ecology* 30: 564-571.

Murray, K. A., Rosauer, D., McCallum, H. & Skerratt, L. F. (2011) Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proceedings of the Royal Society B* 278: 1515-1523.

Olalla-Tárraga, M. Á., McInnes, L., Bini, L. M., Diniz-Filho, J. A. F., Fritz, S. A., Hawkins, B. A., Hortal, J., Orme, C. D. L., Rahbek, C., Rodríguez, M. Á. and Purvis, A. (2011), Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. Journal of Biogeography. *Journal of Biogeography*. 38: 2237-2247.

Pearman, P. B., Guisan, A., Broennimann, O. & Randin, C. F. (2007) Niche dynamics in space and time. *Trends in Ecology and Evolution* 23: 149-158.

Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

Perera, S. J., Ratnayake-Perera, D & Procheş, Ş. (2011) Vertebrate distributions indicate a greater Maputaland- Pondoland- Albany region of endemism. *South African Journal of Science* 107: 15 pages. doi:10.4102/sajs. v107i7/8.462

Reyers, B., Fairbanks, D. K. H & Van Jaarsveld, A. F. (2001) Priority areas for the conservation of South African vegetation: a coarse-filter approach. *Diversity and Distributions* **7**: 79-95.

Rich, T. C. G. & Woodruff, E. R. (1996) Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217-229.

RQS (2010) 1:500000 spatial dataset of rivers of South Africa (June 2010 release). Resource Quality Services, Department of Water Affairs. http://www.dwaf.gov.za/iwqs/gis_data/river/rivs500k.html Cited 21 October 2011

SANBI (2010) South African wetland types, National Wetlands Inventory Version 3, South African National Biodiversity Institute, Pretoria. http://bgis.sanbi.org/nwi/map.asp. Cited 24 October 2011

Schulze, R. E. (Ed.) (2007) South African Atlas of Climatology and Agrohydrology. Water Research Commission, Pretoria, RSA, WRC Report 1489/1/06.

Segurado, P. & Araújo, M. B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31: 1555-1568.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115-1123.

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H. & Bradshaw, C. J. A. (2008) Measuring the Meltdown: Drivers of Global Amphibian Extinction and Decline. *PLoS ONE* 3: 1-8.

Stearns, S. C. (1983) The influence of size and phylogeny on patterns of covariation among life history traits in mammals. *Oikos* 41, 173-187.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. (2004) Status and Trends of Amphibian Declines and Extinctions Worldwide. *Science* 306: 1783-1786.

Thuiller, W., Lavorel, S. & Araújo, M. B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography* 14: 347-357.

USGS (2004) Shuttle Radar Topography Mission, 3 ArcSecond scene. Global Land Cover Facility, University of Maryland.

Whitton, F. J. S., Purvis, A., Orme, C. D. L. & Olalla-Tárraga, M. Á. (2011) Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Global Ecology and Biogeography* 20: no. doi: 10.1111/j.1466-8238.2011.00660.x

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, J., Grytnes, J.- A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M. & Stephens, P. R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13: 1310-1324.

Williams, Y. M., Williams, S. E., Alford, R. A., Waycott, M. & Johnson, C. N. (2006) Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biology Letters* 2: 532-535.

Chapter 6: Conclusions

6.1. Sampling biases in the *SAFAP*

The *South African Frog Atlas Project* dataset suffers from comparable sampling biases and limitations that have been recognised in other biological atlases and collections (Freitag et al., 1998; Dennis et al., 1999; Funk & Richardson, 2002; Parnell et al., 2003; Reddy & Dávalos, 2003; Küper et al., 2006; Romo et al., 2006; Ferreira et al., 2007). As such, the problems and solutions identified for the *SAFAP* have relevance for similar datasets. The most serious biases for biogeographical studies are those that affect measurements of the size, location and dynamics of species geographical distributions. Thus, low sampling intensity, geographic sampling bias and differences in sampling intensity between successive datasets are critical issues.

Low sampling intensity is perhaps the most innocuous of these limitations. Atlases are presence-only datasets, but in many applications, absences are assumed where species have not been detected. The simple construction of species distribution maps from atlas datasets results in a presence-absence delineation (Rondinini et al., 2007). At high sampling intensities, the assumption that non-detections represent true absences is mostly accurate (Tingley & Beissinger, 2009; Robertson et al., 2010). However, at low sampling intensities, species detection probabilities are also low, and non-detections high. The consequence is that range sizes and species richness are underestimated. The *SAFAP*, including both the historical and atlas time-periods, had a sampling intensity of only 3.35 records per 100 km^2. This is more than two orders of magnitude less than the much-utilised *South African Bird Atlas Project* (over 550 records per 100 km^2; Harrison et al., 2008). The lack of volunteer interest in amphibians, and the relative difficulties in surveying frogs, contributed to the poorer sampling effort in the *SAFAP*. According to a species richness assessment, low sampling intensity resulted in potential under-sampling for as many as 64% of the QDGCs in the study region. It follows that a high proportion of the absences in the *SAFAP* are really non-detections. Species will have been sampled only in areas of high abundance, and range sizes will consequently have been underestimated.

Variation in sampling effort over the study area compounds the problems of low sampling intensity. Geographic sampling bias results in differences in species detection probability between regions. Better-sampled areas appear to contain many species with large ranges, relative to poorly sampled areas with fewer, small-range species (Reddy & Dávalos, 2003; Küper et al., 2006). Thus, geographic bias becomes important when comparing biodiversity between regions, as is required for systematic conservation planning. Conservation plans constructed from geographically biased data incorrectly assign priority to well-sampled regions and neglect poorly sampled regions (Williams et al., 2002; Reddy & Dávalos, 2003). Geographic sampling bias was evident within the *South African Frog Atlas Project*. Well-sampled QDGCs were concentrated along the eastern and southern coastlines of South Africa. The arid central and western regions were almost uniformly under-sampled. Within 200 km of cities, 30 km of national roads and 10 km of protected areas, there were significantly more well-sampled QDGCs and more frog presence records than were expected. Researchers focussed their sampling on areas that were conveniently accessible or those with perceived higher biodiversity. The real west-to-east pattern of increased amphibian richness and abundance was exaggerated by the geographic bias confirmed in the *SAFAP*. Thus, species richness and range sizes will be overestimated in the eastern and southern regions where the majority of cities, roads and protected areas are located. The remote, arid western region will have underestimated species richness and range sizes.

Geographic bias affects comparisons of biodiversity in space. Similarly, a temporal difference in sampling intensity complicates comparisons of species range sizes over time. Historical data used as a baseline for comparisons generally has a lower sampling intensity than recent biological atlases. Low sampling intensity in the earlier dataset results in lower detection probabilities and smaller documented range sizes. Increased sampling intensity in later datasets likewise produces larger range sizes. Hence, a typical increase in sampling over time leads to sampling-related apparent range increases (Shoo et al., 2006; Ferreira et al., 2007; Kuussaari et al., 2007). Such false increases can mask the actual range size changes experienced by species. This is significant as range size reductions are an accepted proxy for detecting population declines during IUCN classification (IUCN, 2001; Joseph & Possingham, 2008). The *SAFAP* showed the expected increase in sampling intensity between the historical and atlas datasets. The historical dataset contributed 16 938 records, and achieved a 62% geographical coverage of the study area in 91 years. In contrast, during eight years of systematic sampling, the atlas dataset returned 1.5 times more records and covered 84% of the study area. This substantial increase in sampling intensity had the predicted effect. *SAFAP* species showed erroneous sampling-related increases in range size of approximately 30%.

6.2. Methods to reduce sampling bias

Some potential *SAFAP* users were concerned about poor data quality and unknown biases in the dataset. This investigation has shown that these suspicions are generally valid. There are significant geographic and temporal variations in sampling intensity in the *SAFAP*. Researchers will have to make a determination of whether the dataset is of sufficient quality for their particular application. The quantitative descriptions of sampling bias in the *SAFAP* that are provided here will aid this decision. They may prefer either to wait until possible future atlas projects return superior data, or to apply methods that minimise sampling biases as much as possible.

Two main improvements to future atlases will reduce sampling bias issues. The first is a general increase in sampling intensity. The species discovery curve describes the relationship between species detection and sampling intensity. It increases steeply at low sampling intensities and reaches an asymptote at higher sampling intensities (Rich & Smith, 1996; Elphick, 1997; Williams et al., 2002). At higher sampling intensities, differences in sampling intensity will have a smaller effect on the number of species detected (Williams et al., 2002). Thus, additional targeted sampling in QDGCs identified as under-sampled should return further species presence records, and reduce non-detections. Continuing the tradition of citizen science in South African atlases could provide the necessary human resources to achieve more widespread and thorough sampling (Boakes et al., 2010). Improved recording, particularly of difficult to identify amphibians, may be achieved through training and instruction of interested volunteers (Rich & Smith, 1996). The second improvement is to measure sampling effort. Creating a temporal unit of sampling, such as person hours, is a potential technique by which to achieve this (Robertson et al., 2010). If sampling effort is known, it can be corrected for in subsequent analyses.

Biological atlases will probably never be completely without sampling biases. Many factors cannot be standardised during sampling. Weather, vegetation type, topography, recorder experience and species developmental stage can all affect detection probabilities (Rich & Smith, 1996; Dennis et al., 1999; Tyre et al., 2003; Tingley & Beissinger, 2009). Moreover, the sampling intensity required to eliminate biases is seldom achievable when countered with practical matters (Robertson et al., 2010). However, datasets with low sampling intensity can still be valuable sources of information. Gaston and Rodrigues (2003) found that having some indication of the spatial pattern of biodiversity was much superior for reserve selection than purely random reserve placement. Broad patterns of species richness and range size are often detectable despite sampling biases (Williams et al., 2002; Parnell et al., 2003). The *SAFAP* is still the most comprehensive assessment of amphibian distributions available in South Africa. For a comparatively neglected taxon, it represents a significant contribution to the understanding of the distributions, life histories and taxonomy of South African amphibians.

Since atlases are valuable, common data sources, methods are available that aim to overcome the problems of sampling biases when measuring species range change (Van Swaay, 1990; Rich & Woodruff, 1996; Warren et al., 2001; Telfer et al., 2002; Kuussaari et al., 2007; Tingley & Beissinger, 2009; Boakes et al., 2010). Increased geographic coverage and increased sampling intensity were two primary problems with the *SAFAP* data that these methods had to address adequately. Categorical comparisons, sub-sampling and correction factors were thus applied to the *SAFAP* with varied success.

Two methods were identified that were superior to the others. These two methods were used to control for the effects of sampling bias in the *SAFAP* during further investigations. The Rich and Woodruff (1996) correction factor performed best at measuring the correct sign and magnitude of range change for hypothetical species. It was particularly effective for the critical small-range species and species undergoing range contractions. It achieved this success with minimal removal of records. Thus, this method was used for all further analyses that required a quantitative assessment of range change in *SAFAP* species. The major limitation with correction factors is that they are unsuitable for spatial analyses. The procedures use total range size values and do not correct for differing sampling intensity at a spatial level. Thus, for spatial analyses of the *SAFAP*, a moderate sub-sampling method was selected that limited analyses to those QDGCs with more than five frog presence records. This level of sub-sampling was optimal as it balanced the reduction of false range increases with the minimum necessary data removal (Kuussaari et al., 2007). These two methods are among the best available for addressing differences in sampling intensity between successive datasets. However, some modification or combination of these methods may improve the measurement of empirical range changes from such datasets in the future.

6.3. Range dynamics in South African amphibians

Before any corrections, and even with the inflated sampling-related increases, 38.9% of South African frog species showed range contractions of <−10%. This is relevant because these range contractions are contrary to the apparent range expansions expected when using datasets with increased sampling intensity. Despite higher detection probabilities, these species still had smaller documented range sizes during the later sampling period. These range contractions are probably real and underestimated. Conversely, the 47.8% expanding ranges and 12.4% stable ranges calculated before corrections are questionable. Without adjustment for differing sampling intensities, species with real stable or contracting ranges may have been incorrectly classified as expanding. After the correction factor of Rich and Woodruff (1996) was applied, 60.2% of *SAFAP* species showed range contractions (<−10%), 19.5% showed stable ranges (−10% to 10%) and 19.5% showed range expansions (>10%). Since this method accounted for both increased geographic coverage and increased sampling intensity, and was the most reliable when tested on hypothetical species, these proportions are more credible.

The range contractions documented here for endemic South African species provide data useful for updating IUCN threat status and population trends. The IUCN criteria recognise reductions in species ranges as a surrogate for population declines. Criterion A2c for all categories of threat status states that: "An observed, estimated, inferred or suspected population size reduction... over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on... (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat" (IUCN, 2001). Range size changes in the *SAFAP* were recorded after 1996. Most historical records are from the 1970s and 1980s, although some occurred as early as 1905. Hence, the ten-year limit on this criterion may not be met for some species.

Seventeen endemic South African frog species are officially Threatened (IUCN, 2011). Of these, 15 experienced negative range size change between the historical and atlas sampling periods. Thus, this analysis of *SAFAP* supports the current threat status for these species. The remaining two species were only recently described and have few historical records as a reference for range change. One endemic species (*Amietia vertebralis,* previously named *Strongylopus hymenopus*) may qualify for Critically Endangered status based on a greater than 80% reduction in range size under criterion A2c (IUCN, 2001). Similarly, 14 endemic species showed a range contraction of between 50 and 80% and thus may qualify for Endangered status. Six species may qualify for Vulnerable status based on range size reductions between 30 and 50%. Of the 14 endemic South African species listed by the IUCN as having decreasing populations, this analysis confirms this judgment in 11 cases. However, 17 endemic species currently described as having "stable" populations showed negative range change of <−10% in this analysis. Importantly, this study can also provide estimates of population trends for 18 species with "unknown" population status. Fifteen of these species have contracting ranges <−0.1 and should be described as "decreasing". Two of the remaining three species have "stable" population trends and one was a recently described species with an incomplete historical reference.

Land-cover change has been, and will continue to be, the most significant contributor to biodiversity loss worldwide (Sala et al., 2000; Warren et al., 2001; Foley et al., 2005; Cushman, 2006). Undoubtedly, land-cover change has affected the ranges of South African amphibian species. Land-cover change had transformed 20% of South African land area by 1994/1995 (Fairbanks et al., 2000), with anthropogenic habitat modifications concentrated in the amphibian rich eastern and southern parts of the country. Land transformation may be responsible for the overall range contractions experienced by the majority of frog species. The high proportion of contracting species in the Eastern Escarpment District may be indicative of the high land-transformation in this eastern region. Higher levels of land-cover change in certain parts of species' ranges may cause shifts out of the affected areas as local extirpations occur (Sih et al., 2000; Pocock et al., 2006).

Range shifts in South African frog species were consistent with some climate change hypotheses. Generally, upslope and poleward range shifts are predicted as species disperse into areas where a warming climate will support new populations (Parmesan et al., 1999; McCarty, 2001; Warren et al., 2001; Parmesan & Yohe, 2003; Root et al., 2003; Shoo et al., 2006). Average upslope range shifts for *SAFAP* species of 47.6 m may thus be climate-related. However, as species did not shift significantly along latitudinal gradients, there is no evidence for the similarly predicted poleward range shifts. This validates the theory that southern hemisphere species may show differing responses to climate change to northern hemisphere species. It is possible that local conditions related to precipitation supersede global patterns. The major west-to-east aridity gradient in South Africa is largely responsible for biogeographic patterns of species richness and abundance (Erasmus et al., 2002; Rouget et al., 2004; Evans et al., 2006). The observed shifts of South African frog assemblages towards regions of biome resilience may indicate a local response to climate change. Bushveld species shifted upslope and northwesterly towards the area of Savanna Biome resilience.

Land-cover change, climate change, or interactions between these two factors, are probably responsible for many of the observed range changes in South African frog species. These two widespread threats are doubtless acting on the geographic ranges of South African amphibians. Consequently, declines in South African frog species (60.2%) equals or even exceeds the global proportions of declining amphibians (43%). While South African frogs may have largely escaped catastrophic declines due to natural resistance to chytrid infection, ongoing land-cover changes have altered habitats and climate changes may be restricting species to areas where current biome conditions persist. Cushman (2006) suggests that the role of land-cover change in amphibian declines, whilst generally acknowledged, has received disproportionately less research attention than the dramatic declines documented in pristine habitats. Land-cover changes may be the most important threat to amphibians, in South Africa and globally, and require detailed investigations into the mechanism by which species geographic ranges respond to land transformation (Cushman, 2006). A direct causal mechanism or a dose-response relationship with measured climate variables will also improve confidence in a climate-change response (McCarty, 2001; Carey & Alexander, 2003;

Virkkala et al., 2005). These future research options require reliable land-cover and climate data with a historical perspective. Like atlas data, the many limitations associated with comparability and coverage of historical land-cover (Verburg et al. 2011) and climate data may impede their use in investigations of causal range change.

6.4. Characteristics of species with contracting ranges

There are many predictions about the differing susceptibility of species to declines. Factors hypothesised to affect decline risk include range size, body size, life form, life history, endemicity, niche breadth, range position, range structure, dispersal ability and many others (Kotze & O'Hara, 2003; Murray & Hose, 2005; Broennimann et al., 2006; Okes et al., 2008; Sodhi et al., 2008; Cooper et al., 2008; Bielby et al., 2008; Murray et al., 2011). Life history characteristics may govern the manner in which a species range is changed, by providing the biological mechanisms that can either create a particular distribution pattern or allow it to be created (Pocock et al., 2006). Determining common ecological traits amongst South African amphibians with range contractions thus improved the positive attribution of observed declines to possible causal factors such as land-cover or climate change.

In agreement with studies in other regions and for other taxa (e.g. Kotze & O'Hara, 2003; Murray & Hose, 2005; Cooper et al., 2008; Sodhi et al., 2008; Pöyry et al., 2009; Murray et al., 2011), South African amphibians with small ranges were more likely to have undergone range contractions than those with large ranges ($R^2 = 0.35 – 0.39$). This single trait often has significantly higher predictive power than other life history characteristics for predicting amphibian threat risk (Murray & Hose, 2005; Cooper et al., 2008; Sodhi et al., 2008; Murray et al., 2011). It is possible that small range size is a composite product of many ecological and physiological traits that increase a species risk of declining. At the large scales at which species range limits are defined, niche breadth is the most probable factor influencing range size (Pearson & Dawson, 2003; Soberón, 2007; Hirzel & Le Lay, 2008; Olalla-Tárraga et al., 2011). The variety of conditions that a species can tolerate will generally regulate its distributional area. Ecological Niche Factor Analysis proved to be an ideal method with which to measure relative niche breadth amongst species of the *SAFAP*. Its reliance on presence-only data (Hirzel et al., 2002; Segurado & Araújo, 2004; Basille et al., 2008) ensured that the sampling biases of the *SAFAP* were minimised. ENFA showed that habitat specialists at the scale of the *SAFAP* were few, and primarily related to the Grassland and Fynbos biomes. The many climate specialists were associated with the timing of precipitation, either preferring highly seasonal rainfall, or more regular rainfall.

Niche breadth was also a significant correlate with range size changes ($R^2 = 0.20 – 0.28$). Species with narrow niches were more likely to have suffered range contractions. Niche breadth, however, was not as good a predictor of range contractions as was range size. Other factors such as low abundance, low fecundity and limited mobility may additionally contribute to declines in small-range species (Gaston, 1998; Kotze & O'Hara, 2003; Thuiller et al., 2005; Cooper et al., 2008; Sodhi et al., 2008). Nevertheless, the details of the niche breadth analyses provided much information about the climate and habitat preferences of species that were contracting. Although there were few habitat specialists, their ranges were exclusively concentrated within known areas of endemism. These areas also had significantly higher degrees of land transformation than other regions. All of the habitat specialist species had suffered range contractions under these conditions. This confirms that areas of endemism occurring in highly transformed regions may be a primary arena for the decline, and ultimate loss, of species. Small-range habitat specialists within these areas should receive the highest conservation priority. Among endemic species, climate specialisation was a better predictor of range contractions than habitat specialisation. The possibility that climate anomalies may be contributing to range contractions among endemic climate specialists is a pressing concern that needs to be resolved with the use of climate data.

The *South African Frog Atlas Project* is a valuable contribution to amphibian biogeographic research and conservation planning in South Africa. Despite the inevitable sampling biases that occur in atlases and natural history collections, corrective methods have allowed for the efficient quantification of range change for South African frogs. The range dynamics measured from the *SAFAP* dataset will be useful to conservation assessments and global change research. There is scope for additional investigations that will further extend the value of the *SAFAP*.

6.5. References

Basille, M., Calange, C., Marboutin, E., Anderson, R. & Gaillard, J.- M. (2008) Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. *Ecological Modelling* 211: 233-240.

Bielby, J., Cooper, N., Cunningham, A. A., Garner, T. W. J. & Purvis, A. (2008) Predicting susceptibility to future declines in the world's frogs. *Conservation Letters* 1: 82-90.

Boakes E. H., McGowan P. J. K., Fuller R. J., Chang-qing D., Clark N. E., O'Connor K. & Mace G. M. (2010) Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* 8: e1000385.

Broennimann O., Thuiller W., Hughes G. O., Midgley G. F., Alkemade J. M. R. & Guisan A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* 12: 1079-1093.

Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211-221.

Carey, C. & Alexander, M. A. (2003) Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9: 111-121.

Cushman, S. A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.

Dennis, R. L. H., Sparks, T. H. & Hardy, P. B. (1999) Bias in butterfly distribution maps: the effects of sampling effort. *Journal of Insect Conservation* 3: 33-42.

Elphick, C. S. (1997) Correcting avian richness estimates for unequal sample effort in atlas studies. *Ibis* 139: 189-190.

Erasmus, B. F. N., Van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. & Wessels, K. J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8: 679-693.

Evans, K. L., Van Rensburg, B. J., Gaston, K. J. & Chown, S. L. (2006) People, species richness and human population growth. *Global Ecology and Biogeography* 15: 625-636.

Fairbanks, D. H. K., Thompson, M. W., Vink, D. E., Newby, T. S., Van den Berg, H. M. & Everard, D. A. (2000) The South African Land-cover Characteristics Database: a synopsis of the landscape. *South African Journal of Science* 96: 69-82.

Ferreira, D., Malard, F., Dole-Olivier, M.-J. & Gilbert, J. (2007) Obligate groundwater fauna of France: diversity patterns and conservation implications. *Biodiversity and Conservation* 16: 567-596.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, III F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharick, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005) Global consequences of land use. *Science* 309: 570-574.

Freitag, S., Hobson, C., Biggs, H. C. & Van Jaarsveld, A. S. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on a southern African mammal data set. *Animal Conservation* 1: 119-127.

Funk, V. A. & Richardson, K. S. (2002) Systematic Data in Biodiversity Studies: Use It or Lose It. *Systematic Biology* 51: 303-316.

Gaston, K. J. (1998) Rarity as double jeopardy. *Nature* 394, 229-230.

Gaston, K. J. & Rodrigues, A. S. L. (2003) Reserve Selection in Regions with Poor Biological Data. *Conservation Biology* 17: 188-195.

Harrison, J. A., Underhill, L. G. & Barnard, P. (2008) The seminal legacy of the Southern African Bird Atlas Project. *South African Journal of Science* 104: 82-84.

Hirzel, A. H., Hausser, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology* 83, 2027-2036.

Hirzel, A. H. & Le Lay, G. (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45: 1372-1381.

IUCN (2001) Categories & Criteria (version 3.1). Prepared by the IUCN Species Survival Commission. IUCN, Gland. http://www.iucnredlist.org/static/categories_criteria_3_1. Cited 16 July 2010.

IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2. http://www.iucnredlist.org. Cited 30 January 2012.

Joseph, L. N. & Possingham, H. P. (2008) Grid-based monitoring methods for detecting population declines: Sensitivity to spatial scale and consequences of scale correction. *Biological Conservation* 141: 1868-1875.

Kotze, D. J. & O'Hara, R. B. (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135: 138-148.

Küper, W., Sommer, J. H., Lovett, J. C. & Barthlott, W. (2006) Deficiency in African plant distribution data – missing pieces of the puzzle. *Botanical Journal of the Linnean Society* 150: 355-368.

Kuussaari, M., Heliölä, J., Pöyry, J. & Saarinen K. (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation* 11: 351-366.

McCarty, J. P. (2001) Ecological Consequences of Recent Climate Change. *Conservation Biology* 15: 320-331.

Murray, B. R. & Hose, G. C. (2005) Life-history and ecological correlates or decline and extinction in the endemic Australian frog fauna. *Austral Ecology* 30: 564-571.

Murray, K. A., Rosauer, D., McCallum, H. & Skerratt, L. F. (2011) Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proceedings of the Royal Society B* 278: 1515-1523.

Okes, N. C., Hockey, P. A. R. & Cumming, G. S. (2008) Habitat Use and Life History as Predictors of Bird Responses to Habitat Change. *Conservation Biology* 22: 151-162.

Olalla-Tárraga, M. Á., McInnes, L., Bini, L. M., Diniz-Filho, J. A. F., Fritz, S. A., Hawkins, B. A., Hortal, J., Orme, C. D. L., Rahbek, C., Rodríguez, M. Á. & Purvis, A. (2011), Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *Journal of Biogeography*. 38: 2237-2247.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Parmesan, C., Ryrhom, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kalla, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. S. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Parnell, J. A. N., Simpson, D. A., Moat, J., Kirkup, D. W., Chantaranothai, P., Boyce, P. C., Bygrave, P., Dransfield, S., Jebb, M. H. P., Macklin, J., Meade, C., Middleton, D. J., Muasya, A. M., Prajaksood, A., Pendry, C. A., Pooma, R., Suddee, S. & Wilkin, P. (2003) Plant collecting spread and densities: their potential impact on biogeographical studies in Thailand. *Journal of Biogeography* 30: 193-209.

Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

Pocock, M. J. O., Hartley, S., Telfer, M. G., Preston, C. D. & Kunin, W. E. (2006) Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology* 94: 581-596.

Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M. & Saarinen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. Global Change Biology 15: 732-743.

Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography* 30: 1719-1727.

Rich, T. C. G. & Smith, P. A. (1996) Botanical recording, distribution maps and species frequency. *Watsonia* 21: 155-167.

Rich, T. C. G. & Woodruff, E. R. (1996) Changes in the vascular plant floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217-229.

Robertson, M. P., Cumming, G. S. & Erasmus, B. F. N. (2010) Getting the most out of atlas data. *Diversity and Distributions* 16: 363-375.

Romo, H., García-Barros, E. & Lobo, J. M. (2006) Identifying recorder-induced geographic bias in an Iberian butterfly database. *Ecography* 29: 873-885.

Rondinini, C., Wilson, K. A., Biotani, L., Grantham, H. & Possingham, H. P. (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters* 9: 1136-1145.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.

Rouget, M., Reyers, B., Jonas, Z., Desmet, P., Driver, A., Maze, K., Egoh, B., Cowling, R. M., Mucina, L. & Rutherford, M. C. (2004) South African National Spatial Biodiversity Assessment 2004: Technical Report. Volume 1: Terrestrial Component. South African National Biodiversity Institute, Pretoria.

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Segurado, P. & Araújo, M. B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31: 1555-1568.

Shoo, L. P., Williams, S. E. & Hero, J.-M. (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology* 31: 22-29.

Sih, A., Jonsson, B. G. & Luikard, G. (2000) Habitat loss: ecological, evolutionary and genetic consequences. *TRENDS in Ecology and Evolution* 15: 132-134.

Soberón, J. (2007), Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115-1123.

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H. & Bradshaw, C. J. A. (2008) Measuring the Meltdown: Drivers of Global Amphibian Extinction and Decline. *PLoS ONE* 3: 1-8.

Telfer, M. G., Preston, C. D. & Rothery, P. (2002) A general method for measuring relative change in range size from biological atlas data. *Biological Conservation* 107: 99-109.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography* 14: 347-357.

Tingley, M. W. & Beissinger, S. R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution* 24: 625-633.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K. & Possingham, H. P. (2003) Improving Precision and Reducing Bias in Biological Surveys: Estimating False-Negative Error Rates. *Ecological Applications* 13: 1790-1801.

Van Swaay, C. A. M. (1990) An assessment of the changes in butterfly abundance in the Netherlands during the 20th Century. *Biological Conservation* 52: 287-302.

Verburg, P. H., Neumann, K. & Nol, L. (2011) Challenges in using land use and land cover data for global change studies. *Global Change Biology* 17: 974-989.

Virkkala, R., Luoto, M., Heikkinen, R. K. & Leikola, N. (2005) Distribution patterns of boreal marshland birds: modelling the relationships to land cover and climate. *Journal of Biogeography* 32: 1957-1970.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C. D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.

Williams, P. H., Margules, C. R. & Hilbert, D. W. (2002) Data requirements and data sources for biodiversity priority area selection. *Journal of Bioscience* 27: 327-338.

Appendix

Table 5: A list of the 113 species recorded in the *SAFAP*. The 'Species name' is the updated taxonomy after Frost et al. (2006) and used in the field guide of Du Preez & Curruthers (2009). Asterisks (*) indicate species endemic to the study area. 'Conservation status' and 'Population status' are from the most recent IUCN assessment for each species (IUCN, 2011). The 'Range change (correction factor)' is the change in species range size between the historical and recent sampling periods, after the application of the correction factor as stipulated in Rich and Woodruff (1996). 'Range change (>5 sub-sampling)' is the proportional range change calculated from only those QDGCs with more than five presence records. 'Range shift distance' is the distance (km) that the mean centre of the species ranges moved between the historical and recent sampling periods, and 'Range shift direction' gives the bearing (°) along which this shift occurred. 'Habitat niche breadth' and 'Climate niche breadth' give the overall Tolerance factors for each species from the ENFA (a value close to 0 indicates a specialist and a value close to 1 a generalist).

Species name (Du Preez & Curruthers, 2009)	**Conservation status 2011** (IUCN)	**Population status 2011** (IUCN)	**Range size change** (correction factor)	**Range size change** (>5 sub-sampling)	**Range shift distance** (km)	**Range shift direction** (°)	**Climate niche breadth** (Tolerance)	**Habitat niche breadth** (Tolerance)
Afrixalus aureus	LC	stable	-0.24	0.09	28.54	344.43	0.22	0.52
Afrixalus delicatus	LC	decreasing	-0.11	0.18	90.28	33.24	0.16	0.58
Afrixalus fornasinii	LC	stable	-0.27	-0.04	12.64	229.35	0.22	0.57
Afrixalus knysnae*	EN	unknown	-0.25	-0.25	11.42	68.53		
Afrixalus spinifrons*	NT	unknown	-0.78	-0.71	54.80	210.12	0.18	0.66
Amietia angolensis	LC	stable	-0.20	-0.13	20.98	82.16	0.86	0.90
Amietia dracomontana*	LC	stable	-0.50	-0.38	48.20	96.29		
Amietia fuscigula	LC	stable	0.09	0.19	62.31	34.15	0.86	0.80
Amietia umbraculata*	NT	unknown	-0.49	-0.25	0.76	353.08	0.18	0.11
Amietia vandijki*	LC	stable	0.75	0.00	25.51	269.91		
Amietia vertebralis*	LC	unknown	-0.85	-0.78	111.99	206.42	0.14	
Amietophrynus garmani/poweri	LC	stable	0.19	0.28	51.87	295.94	0.38	0.88
Amietophrynus gutteralis	LC	increasing	0.04	0.11	40.70	316.71	0.59	0.86
Amietophrynus maculatus	LC	stable	-0.03	0.18	9.05	261.03	0.29	0.77
Amietophrynus pantherinus*	EN	unknown	-0.36	-0.14	17.13	128.62		

Amietophrynus pardalis*	LC	decreasing	-0.61	-0.52	89.41	239.69	0.16	0.59
Amietophrynus rangeri*	LC	decreasing	-0.28	-0.21	133.18	212.30	0.91	0.85
Anhydrophryne hewitti*	LC	stable	-0.79	-0.70	51.81	208.11	0.20	0.33
Anhydrophryne ngognoniensis*	EN	stable	2.00	3.00	34.49	247.94		
Anhydrophryne rattrayi*	EN	decreasing	-0.70	-0.60	45.96	70.73		
Arthroleptella bicolor*	LC	stable	-0.25	0.00	6.33	359.86		
Arthroleptella drewesii*	NT	unknown	-0.25	0.00				
Arthroleptella landdrosia*	NT	stable						
Arthroleptella lightfooti*	NT	unknown	-0.25	0.00				
Arthroleptella villiersi*	LC	stable	0.07	0.43	10.96	312.91		
Arthroleptis stenodactylus	LC	stable	-0.47	-0.30	161.15	165.16	0.13	0.24
Arthroleptis wahlbergi*	LC	decreasing	0.06	0.19	22.39	30.24	0.18	0.62
Breviceps acutirostris*	LC	stable	0.29	0.57	9.57	141.30	0.10	
Breviceps adspersus	LC	stable	-0.02	-0.03	65.76	345.51	0.67	0.92
Breviceps bagginsi*	VU	unknown	1.25	1.00	73.46	224.24		
Breviceps fuscus*	LC	stable	-0.46	-0.33	19.36	254.94		0.41
Breviceps gibbosus*	NT	unknown	-0.08	0.00	8.93	341.39		
Breviceps macrops	VU	decreasing	-0.25					
Breviceps montanus*	LC	stable	0.79	1.00	45.33	79.83	0.36	0.53
Breviceps mossambicus	LC	stable	0.91	1.19	38.05	287.40	0.37	0.62
Breviceps namaquensis*	LC	stable	-0.32	-0.43	23.54	2.05	0.25	
Breviceps rosei*	LC	stable	0.05	0.17	71.92	308.50	0.19	
Breviceps sopranus*	LC	stable	0.20	0.60	2.38	327.98	0.10	
Breviceps sylvestris*	EN	unknown	-0.16	0.17	24.31	3.02		0.22
Breviceps verrucosus*	LC	stable	-0.11	0.08	76.07	49.06	0.43	0.64
Cacosternum boettgeri	LC	unknown	0.56	0.73	24.97	26.78	0.88	0.94
Cacosternum capense*	NT	decreasing	-0.13	-0.06	13.51	2.66	0.18	
Cacosternum karooicum*	LC	stable	-0.57	-0.40	69.65	325.69	0.08	
Cacosternum namaquense	LC	stable	0.03	0.00			0.24	
Cacosternum nanum*	LC	stable	0.81	0.91	24.95	220.18	0.61	0.78
Cacosternum parvum*	LC	stable	-0.53	-0.50	102.67	10.00	0.14	0.16
Cacosternum poyntoni*	DD	unknown	-1.00	-1.00				
Cacosternum striatum*	LC	stable	-0.77	-0.70	67.06	250.22	0.08	0.18

Capensibufo rosei*	VU	unknown	-0.62	-0.44	10.15	236.67		
Capensibufo tradouwi*	LC	decreasing	-0.62	-0.57	130.79	276.24	0.25	0.11
Chiromantis xerampelina	LC	unknown	-0.08	0.13	48.31	283.42	0.38	0.77
Hadromophryne natalensis*	LC	decreasing	-0.65	-0.49	85.57	353.87		0.52
Heleophryne hewitti*	EN	unknown	-0.25	0.00			0.36	
Heleophryne orientalis*	LC	stable	-0.62	-0.75	12.75	89.91		
Heleophryne purcelli*	LC	stable	-0.36	-0.25	46.81	327.60	0.28	
Heleophryne regis*	LC	stable	-0.65	-0.55	39.10	280.04		0.11
Heleophryne rosei*	CR	stable	-0.25	0.00				
Hemisus guineensis broadleyi	LC	unknown	-1.00	-1.00				
Hemisus guttatus*	VU	unknown	-0.60	-0.43	72.80	336.87	0.20	0.52
Hemisus marmoratus	LC	unknown	0.02	0.21	25.92	280.45	0.34	0.65
Hildebrandtia ornata	LC	stable	-0.51	-0.41	38.75	283.54	0.26	
Hyperolius acuticeps	LC	decreasing	-0.60	-0.53	118.63	214.78	0.16	0.53
Hyperolius argus	LC	decreasing	-0.45	-0.27	26.85	27.20	0.17	0.52
Hyperolius horstockii*	VU	decreasing	-0.04	0.13	24.21	112.67	0.14	0.45
Hyperolius marmoratus	LC	increasing	0.28	0.46	58.61	240.48	0.63	0.88
Hyperolius pickersgilli*	CR	unknown	-0.62	-0.50	39.77	214.35		
Hyperolius pusillus	LC	stable	-0.07	0.14	50.00	173.05	0.38	0.73
Hyperolius semidiscus*	LC	decreasing	-0.28	-0.17	115.15	222.39	0.40	0.79
Hyperolius tuberilinguis	LC	stable	0.07	0.40	23.09	198.92	0.29	0.62
Kassina maculata	LC	unknown	0.05	0.43	32.85	183.80	0.26	0.62
Kassina senegalensis	LC	stable	0.85	0.77	21.64	218.25	0.65	0.92
Leptopelis mossambicus	LC	decreasing	-0.06	0.28	44.98	176.29	0.31	0.64
Leptopelis natalensis*	LC	decreasing	-0.07	0.07	0.67	26.41	0.11	0.56
Leptopelis xenodactylus*	EN	unknown	-0.37	-0.20	9.19	352.12		
Microbatrachella capensis*	CR	decreasing	-0.57	-0.43	23.17	119.95		
Natalobatrachus bonebergi*	EN	decreasing	-0.78	-0.75	112.08	210.99	0.09	0.34
Phrynobatrachus acridoides	LC	stable	-1.00	-1.00				
Phrynobatrachus mababiensis	LC	stable	-0.23	0.01	33.21	143.38	0.41	0.78
Phrynobatrachus natalensis	LC	stable	-0.41	-0.32	76.31	67.82	0.57	0.85
Phrynomantis annectens	LC	stable	-0.25	-0.50	166.71	274.41		
Phrynomantis bifasciatus	LC	stable	0.19	0.40	34.91	339.08	0.38	0.83

___Poyntonia paludicola*___	NT	stable	-0.36	-0.14	3.09	100.83		
___Poyntonophrynus fenoulheti___	LC	stable	-0.76	-0.67	39.76	335.60	0.34	0.75
___Poyntonophrynus vertebralis*___	LC	unknown	0.00	0.18	52.03	317.15	0.38	0.71
___Ptychadena anchietae___	LC	stable	0.18	0.25	39.82	281.94	0.39	0.84
___Ptychadena mascareniensis___	LC	stable	-0.81	-0.75	35.61	192.59	0.17	0.47
___Ptychadena mossambica___	LC	stable	0.18	0.36	97.70	278.48	0.35	0.74
___Ptychadena oxyrhynchus___	LC	stable	0.00	0.14	10.88	4.46	0.42	0.73
___Ptychadena porosissima___	LC	stable	0.19	0.22	75.27	242.59	0.43	0.63
___Ptychadena taenioscelis___	LC	stable	-1.00	-1.00			0.09	0.17
___Ptychadena uzungwensis___	LC	unknown	-1.00	-1.00				
___Pyxicephalus adspersus___	LC	decreasing	-0.48	-0.25	56.85	302.13	0.61	0.87
___Pyxicephalus edulis___	LC	stable	-0.12	0.04	107.38	308.76	0.38	0.71
___Schismaderma carens___	LC	unknown	-0.27	-0.22	35.05	313.74	0.42	0.80
___Semnodactylus wealii*___	LC	stable	0.76	0.69	33.10	166.71	0.64	0.69
___Strongylopus bonaespei*___	LC	stable	-0.50	-0.37	42.74	273.72	0.28	0.47
___Strongylopus fasciatus___	LC	stable	-0.13	0.01	30.47	354.43	0.71	0.81
___Strongylopus grayii*___	LC	stable	-0.04	0.04	4.26	269.60	0.87	0.83
___Strongylopus springbokensis*___	LC	stable	-0.36	-0.33	47.19	327.01		
___Strongylopus wageri*___	LC	stable	-0.73	-0.90	121.45	225.82	0.17	
___Tomopterna cryptotis___	LC	stable	0.31	0.37	22.21	290.26	0.46	0.91
___Tomopterna delalandii*___	LC	stable	0.99	0.83	25.08	357.61	0.61	0.59
___Tomopterna krugerensis___	LC	stable	-0.73	-0.81	76.91	232.01	0.33	0.69
___Tomopterna marmorata___	LC	unknown	-0.09	0.30	30.59	187.99	0.18	0.55
___Tomopterna natalensis___	LC	stable	0.17	0.22	9.70	305.61	0.47	0.76
___Tomopterna tandyi___	LC	stable	2.60	2.91	100.71	30.90		
___Vandijkophrynus amatolicus*___	CR	decreasing	-0.81	-0.75	18.05	135.04		
___Vandijkophrynus angusticeps*___	LC	decreasing	-0.56	-0.49	67.42	330.42	0.47	0.55
___Vandijkophrynus gariepensis___	LC	stable	-0.29	-0.30	112.87	250.04	0.77	0.73
___Vandijkophrynus robinsoni*___	LC	stable	2.16	3.00	147.85	152.83		
___Xenopus gilli*___	EN	unknown	-0.62	-0.50	11.37	243.56		
___Xenopus laevis___	LC	increasing	0.08	0.03	60.91	9.72	0.95	0.91
___Xenopus muelleri___	LC	stable	-0.41	-0.31	52.02	169.55	0.29	0.59