Predictive Modelling for Anuran Responses to Climate Change in Tropical Montane Ecosystems.

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“***The question is not whether such communities exist but whether they exhibit interesting patterns, about which we can make generalizations***” (MacArthur, 1971).

Abstract

Climate change poses a serious threat to many species globally. Potential responses are shifting range, adapting (e.g., phenological changes) or face extinction. Tropical montane ecosystems are particularly vulnerable to shifts in future climate due to rapid land use change, high population growth and multiple changes in the climate system, such as shifts and intensity of seasonality. Climate Change Vulnerability Assessment (CCVA) through Species Distribution Modelling (SDMs) provides a means of spatially assessing the potential impact of climate change on species ranges, but SDMs are limited in application by incomplete distribution data, a particularly acute challenge with rare and narrow ranging species. Malagasy amphibians exemplify the problems of SDMs in CCVA: two-thirds (166 species) have insufficient distribution data to run an SDM. This thesis developed a Trait Distribution Model (TDM) framework to spatially assess the climate-change vulnerability of data-poor, threatened Malagasy amphibians for the first time. By grouping species into trait complexes and then pooling distribution records, TDMs were used to assess the distributions of amphibian communities along environmental gradients. Threatened species clustered into three complexes; arboreal specialists, understorey species and habitat specialists. TDMs predicted the spatial distribution of all species in the landscape, but that ability improved as species' range sizes and distribution data decreased. Correlations between trait complexes and water deficit suggested high levels of climate vulnerability for Malagasy amphibians by 2085, particularly arboreal species. However, omission of habitat variables led to spatial over-prediction, by up to 60%, for specialised species under current climate conditions. Subsequent 'climate+habitat' models revealed that up to eight threatened amphibian species face heightened extinction risk from climate change. Species losses are concentrated in lowland and mid-altitudinal zones, with no projected losses of tropical montane species. TDMs can indicate habitat management at the community level and be part of conservation planning under projected climate change.

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Author's declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapters 2, 3, and 4 have been written as scientific papers. Colleagues and Supervisors are included as co-authors, with contributions across the thesis as follows:

Chapter 1. I wrote the chapter with supervision from Phil Platts and Rob Marchant.

Chapter 2 has been written in the style of Nature Climate Change; I conceived, designed, collected and analysed data and wrote the chapter; Phil Platts: concept, review and editing; Wendy Foden: review and editing; Rob Marchant: concept, review and editing.

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Chapter 1. General Introduction

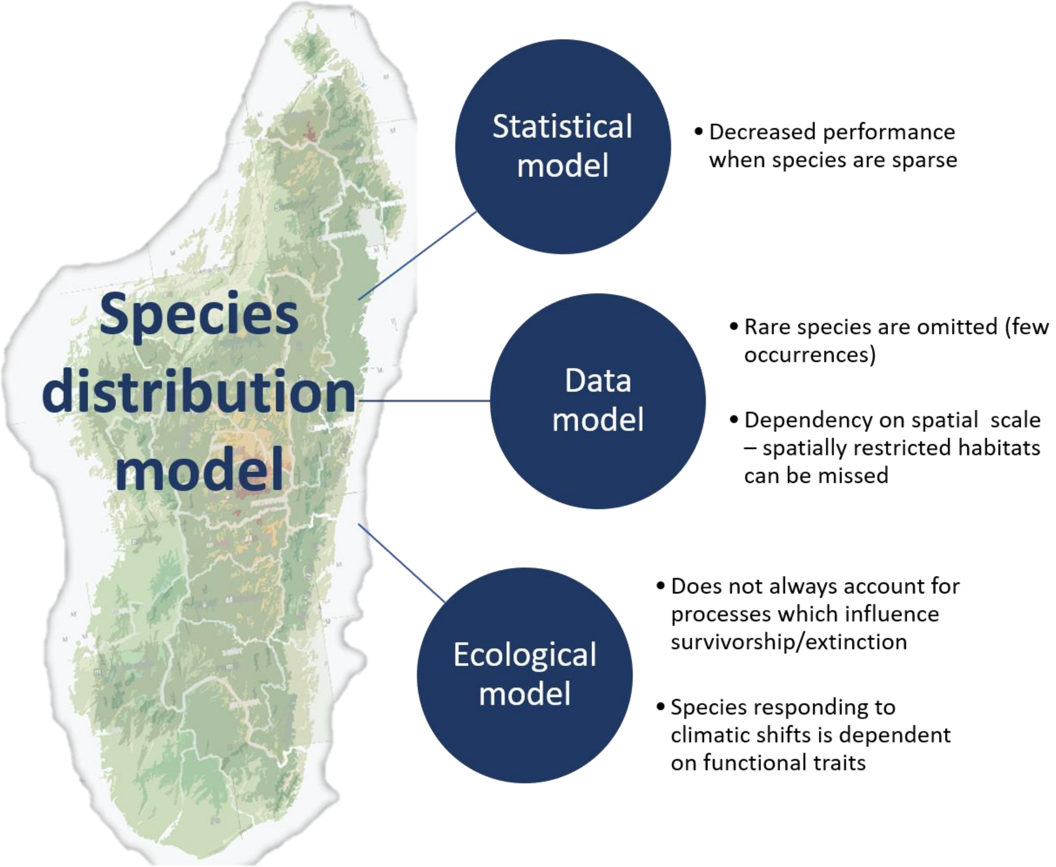
1.1 Overview

Climate change is among the dominant emerging threats to biodiversity in the 21st century. Although habitat loss, pollution, over-hunting and other anthropogenic pressures have already exerted a toll on global biodiversity, climate change is likely to exacerbate the situation, pushing many species already on the brink of extinction over the edge. Therefore, climate change poses and will continue to present a significant and serious threat for ecosystems. Practical actions are needed in order to respond to this growing pressure (Mawdsley *et al*., 2009; Shoo *et al.*, 2011) and this is particularly true for species in restricted habitats, such as tropical montane ecosystems, which are perceived as highly vulnerable to climatic shifts (Peters and Darling, 1985). However, to inform practical actions, then we need to understand how species will respond to future climate change in such habitats. One possible response is to conduct spatial Climate Change Vulnerability Assessment (CCVA) by using Species Distribution Models (SDMs), which have potential to inform conservation planning. But incomplete distribution data limits SDMs for rare and threatened species, omitting them from spatial CCVA. Taxa, such as amphibians, particularly those in Madagascar, exemplify the issues surrounding SDMs and restricted habitats and act as an exemplar throughout this thesis. This thesis investigates a novel method of spatial CCVA, developed to include rare or threatened species and so better to inform conservation decisions. The introduction reviews and discusses the function and limitations of SDMs, the relationship between amphibians and their environment/specific ecosystems, then looks specifically at Malagasy amphibians. Finally, I give a brief overview of the data chapters.

1.2 Species Distribution Models

Species Distribution Models, (SDMs) are a useful tool in climate science (Araújo, 2009). At the most simplistic level, SDMs adopt a correlative approach, using environmental variables and species occurrences to predict species responses to those variables (especially climate), across a landscape, the results of which can be mapped using a Geographic Information System (GIS). The basic framework for SDMs has three components: "... an ecological model, a data model, and a statistical model" (Fig. 1) (Austin, 2002).

Fig. 1. Conceptual diagram of Austin's (2002) Species Distribution Model (SDM) framework, used to outline some limitations of the SDM approach. SDMs have three core components: a statistical model, a data model and an ecological component. Each component has limitations which makes modelling rare species in geographically constrained habitats difficult.



1.2.1 Statistical model

The statistical model has developed and diversified in the past two decades (Guisan and Rahbek, 2011) and now an array of techniques are available to researchers wishing to project species distributions whether, for example, to infer the impact of climate or for distribution of resources for conservation. Typical methods available range from logistic regression to multiple regression (including Generalised Linear Models), discriminant analysis, artificial neural networks, ordination and classification methods, Bayesian models, locally weighted approaches (e.g. General Additive Model), environmental envelopes to name a few (Manel *et al*., 1999; Guisan and Zimmermann, 2000; Miller and Franklin, 2002; Segurado *et al*., 2004). This diversity of techniques can lead to variability in model outcomes, making model selection an important initial step in undertaking any modelling project (Kujala *et al.*, 2013; Warton and Aarts, 2013). Bioclimatic models are recommended within a model hierarchy of increasing complexity (Hannah *et al.*, 2005; Carroll, 2007; Lomba *et al.*, 2010; Grenouillet *et al.*, 2011; Guisan and Rahbek, 2011). But to overcome variability, ensemble forecasting is sometimes employed, where a consensus is taken between model outcomes (Kujala *et al.*, 2013), but by and large selection of single models is highly influenced by the type of data available.

All too frequently researchers are restricted to presence-only distributions (Austin, 2007) which require the generation of pseudo-absences to demarcate the background characteristics of the region for modelling. The exiguous data associated with rare or narrow range endemics necessitates the generation of pseudo-absences and particular care needs to be taken in the placement of these data; methods which avoid bias between environmental and spatial pseudo-absences have been absent from studies until recently (Senay *et al*., 2013). Models often cope with the lack of absence points through pseudo-absences created from environmental background layers, but the selection of these pseudo-absences will affect model outcomes (Elith *et al.*, 2006; Warton and Aarts, 2013). Valid absences can be fitted for more sessile organisms, however cryptic species and those with large seasonal variations will compound the problem (Guisan and Thuiller, 2005). How models cope with absence points in situations with presence-only data has provided recent debate within the literature. Multivariate approaches are suggested for pseudo-absences (Hirzel *et al.*, 2002) or alternatively a suggested method is to employ Point Process Models (PPM). In PPM the number and location of absences are chosen as part of a mathematical construct and supply a measure of the goodness of fit, something that has been absent from processes such as MaxEnt (Phillips *et al*., 2006; Warton and Aarts, 2013). However, MaxEnt is a presence-only technique which is recognised to perform well with presence-only data (Hernández *et al.*, 2006; Raes and ter Steege, 2007; Pearson, 2010) and estimates an index of relative suitability for each grid cell (Phillips *et al*., 2006; Anderson and Gonzalez, 2011; Royle *et al.*, 2012). MaxEnt is a widely used technique in studies with presence-only data and is perhaps viewed as a 'silver-bullet' for such data, but methods to control for record bias are rarely used (Yackulic *et al*., 2013). However, there are several methods that can be implemented in MaxEnt to reduce bias (Syfert *et al*., 2013; Fourcade *et al.*, 2014; Radosavljevic and Anderson, 2014). For example, users can reduce over-fitting through manipulation of the regularization multiplier (β) (Warren *et al*., 2010; Warren and Seifert, 2011), sample one occurrence per grid cell to reduce spatial aggregation (Fourcade *et al.*, 2014) and through kernel density maps (an indication of sampling intensity; Elith *et al*., 2010; Fourcade *et al.*, 2014). Once bias reduction is implemented and the MaxEnt model run, performance is typically assessed by Area Under the Curve (AUC) where, stating rather simplistically, the closer to 1, the better the model. However, the reliability of AUC as an assessment statistic is questionable (Yackulic *et al.*, 2013), particularly with respect to commission and omission errors (Lobo *et al*., 2008) i.e. the balance between the true positive rate (sensitivity; correctly identifying the species in question) and the true negative rate (specificity; correctly identifying the absence of the species in question). Therefore, other measures provide a valuable marker to model performance such as True Skills Statistic (TSS) which is independent from prevalence and reflects sensitivity and specificity (Allouche *et al*., 2006).

Arguably, SDMs allow conservation practitioners the ability to take informed action when managing habitats for species but SDMs are limited by their assumptions, which may hinder spatial projections for some taxa or species. For example, practitioners using SDMs may assume that species retain unlimited dispersal ability and ecological interactions play a minimal role in geographic ranges (Jeschke and Strayer, 2008). While simple SDMs may produce a 'good fit' for large assemblages of species (widely dispersed, mobile, generalists) (Carroll, 2007; Ficetola *et al.*, 2010) the lack of biological realism is detrimental to projections involving rare species. Rare species fall outside SDM assumptions through restricted geographic ranges, are often habitat specialists and can be locally abundant but not, by definition, regionally abundant (Rabinowitz, 1981; Hernandez et al. 2006; Lomba et al. 2010). Ironically, the very attributes that make species rare and necessitate conservation action, of which species distribution modelling is a critical tool (Hernández *et al.*, 2006; Tabor and Williams, 2010), also hinder the modeller; rare species are not only rare biologically, but also demonstrate paucity of data (Hernández *et al.*, 2006; Lomba *et al.*, 2010).

Therefore, we are presented with a paradox: how to apply spatial modelling for CCVA to the group of species which really need it?

1.2.2 Data model

Rare or threatened species are an issue for SDMs because they have few presences and a lack of absences (Engler *et al*., 2004; Lomba *et al.*, 2010), and consequently many such species are deemed ineligible for modelling and thus omitted from spatial CCVA (Platts *et al*., 2014). Not only does this lack of data have implications for the statistical model for threatened species, it also impacts the spatial scale at which the SDM is performed. Many predictions of species response to climate change have been made at a global scale (Hannah *et al*., 2002) but the effect of scale in SDMs receives relatively little consideration (Trivedi *et al.*, 2008). Yet as an ecological concept, scale is essential in explaining the distribution of species. Because of the way species experience their environment, scale needs to be relevant to the species being modelled (Harvey and Weatherhead, 2006; Potter *et al.*, 2013). Thus, regional scale (50 km resolution) may work for large, migratory species (or species with large areas of occupancy) but for species with restricted ranges or in geographically constrained or heterogeneous habitats, regional scale is unlikely to produce relevant results. Coarse-grained models easily ignore landscape metrics relevant to the species in question. For example, topographic refugia in highly heterogeneous habitats can easily be overlooked which is an issue because refugia/microhabitat are known to mediate local climate (Dobrowski, 2011). Conversely, for data-poor or threatened species, the more fine grained the scale, the less likely a presence will be recorded in a grid cell (Engler *et al.,*2004). Thus, for species in restricted habitats, such as tropical montane systems, SDMs run at an inappropriate spatial scale will miss both subject and habitat. The preference of modellers may be to shift to ever increasing resolution, improving the grain and capturing microhabitat nuances which influence niches. However, the casual inference of saying coarse grain is bad, fine is good, is potentially misleading and liable to miss generalised patterns which influence species distributions. Each spatial scale helps to define the distribution of resources, which in turn influence species distributions (Mackey and Lindenmayer, 2001). Thus, drivers of resources at a continental scale influence drivers at subsequent, nested, scales (McMahon *et al.*, 2011).

There are two main types of data used in SDMs: environmental data and species occurrences. Overall, data choice is typically driven by purpose, scale of study and availability of data but purpose, availability of data and the cost of surveys all limit the types of data models that can be adopted (Austin, 2007). Ideally, an exercise in SDM would utilise fresh data, specific for the species or multiple species in question. By doing so the researcher, through experimental design, would retain control over the grain and extent of data (i.e. the spatial scale). For many conservation organisations, the luxury of specific data over large extents are often not possible due to lack of human resources, practicality, timelines and economic constraints (Ward *et al.*, 2009). Therefore, pragmatism drives data choice and there is a need for a technique of spatial CCVA which utilises databases and/or researcher contributed occurrences to identify at risk species, which can then receive further attention. However, choice of data sources has implications in model validity and may introduce un-recognised bias which in turn complicates translation of results. The issue with adopting existing datasets (species occurrences) is that the researcher may be faced with data that suffer from location inaccuracy (Franklin, 2009) and/or be based on poorly designed surveys or opportunistic sightings (sample selection bias) leading to bias correlating with the accessibility of the area surveyed, proximity of roads and other tracks (Austin, 2007); in other words, some areas are more intensively sampled than others (Elith *et al.*, 2011). Databases, therefore, need to be carefully filtered prior to use (Beck *et al.*, 2014) to reduce such bias and errors.

Environmental predictors derived from remote sensing data are common within modelling (He *et al.*, 2015), particularly climate data (Hijmans *et al.*, 2005). But because of the way fine scale climate data are derived, care needs to be taken in selecting appropriate datasets. General circulation models (GCM) express processes from the atmosphere and oceans to provide the umbrella data for climate change (Foden *et al.*, 2018), but pixel resolution does not reflect more localised processes. Therefore, a single value represents a pixel and a pixel covers a large geographic area, which is often incongruent with the object of study (Carey *et al.*, 2001; Potter *et al.*, 2013). Furthermore, GCM outputs differ, so the use of multiple models to understand uncertainty is essential (Foden *et al.*, 2018) particularly as projections are conditional on our current knowledge (Kujala *et al.*, 2013). Regional climate models (RCMs) at finer spatial resolutions are nested within GCMs, but still operate at a spatial scale at an order of magnitude often far greater than either species or habitat (e.g. c. 50 km), limiting RCM application in ecology (Platts *et al*., 2015). To bridge the spatial gap from climate data (Potter *et al.*, 2013), this thesis uses the AFRICLIM dataset which considers eight GCMs dynamically downscaled using two RCMs at multiple high-spatial resolutions (c. 1 km) (Platts *et al*., 2015).

Whilst climate data are commonly derived from remote sensing, the use of remote sensing is also becoming increasingly common in documenting habitat characteristics for use in species research (Requena-Mullor *et al.*, 2017), as such data more than suitably reflects environmental processes (e.g. changes in vegetation characteristics over large extents; Deblauwe *et al.*, 2016). Furthermore, technological improvements, such as 'active' sensing (e.g. LIDAR or RADAR), are providing new predictors through metrics such as canopy structural diversity (Goetz *et al.*, 2007; He *et al.*, 2015) and canopy height (Simard *et al.*, 2011). Products from passive sensing cover other vegetation or land-use attributes, from land-cover maps (e.g. GLOBCOVER), to leaf-area index (Pfeifer *et al.*, 2012a) and vegetation indices (e.g. normalized difference vegetation index) (Pfeifer *et al.*, 2012b). The latter can act as a proxy for food availability or shelter (He *et al.*, 2015) and is likely to be an important determinant of distribution where species or taxa are intrinsically linked to habitats (Cushman, 2006).

1.2.3 Ecological model

Assumptions of relationships made at the ecological level regarding the nature of environmental predictors play an integral, and sometimes conflicting, role much later in the modelling process (Austin, 2002; Vaz *et al.*, 2007). Ecological relationships are typically non-linear (Austin, 2002) and ecological theory predicts that population growth of a species is determined by the most limiting resource not medians or means (Hiddink and Kaiser, 2005; Vaz *et al.*, 2007). Despite these boundaries, the modelling environment still fails to reflect the fundamental niche to the landscape (Pearson and Dawson, 2003; Kearney *et al.*, 2008).

The aberration between modelling and ecological theory fails to account for processes which influence survivorship/extinction (Shoo *et al.* 2005; Keith *et al.*, 2008), while the probability of a species adapting to climatic shifts is dependent on species traits (Foden *et al.*, 2008, 2013). The appearance of species traits in a community is the result of filtration. Inclusion of a species into a community is governed by a set of filters (Keddy, 1992; Poff, 1997; Cornwell *et al.*2006; Ferrier and Guisan, 2006); abiotic and biotic filters remove the least-suited species and the remaining species survive and reproduce (Keddy, 1992). Functional traits ('species traits' or 'traits' are used here interchangeably) are analogous to species: those traits beneficial to survival and reproduction are kept within a community, others are filtered out. Thus, species traits offer an insight into natural selection and the resulting community structure. Furthermore, traits can help us to understand the response of rare or threatened species to the environment; if a rare species exhibits a trait that is congruous to the abiotic and biotic filters, it will be included within the community structure. Traits also capture eco-physiological processes and aspects of life-history strategies which are relevant for spatial scales required for fine-scale modelling (Adler *et al.*, 2013). Therefore, species traits hold valuable information about a species' potential response to climate and provide an avenue of research that would be valuable in spatial CCVA.

The difficulty with including species traits in modelling is that such trait-based models are complex and require improved datasets (Nicholson *et al.*, 2006; Pöyry *et al.*, 2008; Araújo, 2009) from which more robust projections can be made (Roberts and Hamann, 2012). A growing movement towards process-based (as opposed to correlative) models which incorporate ecological theory (including species traits) are yielding more robust results and improved translation (Maschinski *et al.*, 2006; Nicholson *et al.*, 2006; Saltz *et al*., 2006; Golicher and Cayuela, 2007; Keith *et al.*, 2008; Anderson *et al.*, 2009; Kearney and Porter, 2009). But these models tend to be focussed on single species where enough data exists (or can be collected) on life history traits, such as dispersal or life stage mortality, and are anchored in phylogenetic analysis (Freckleton *et al.* 2002; Ostman and Stuart-Fox, 2011). Such processed-based models with detailed life history traits may well provide much needed ecological realism and improved projections (Akçakaya *et al.*, 2004; Pöyry *et al.*, 2008; Anderson *et al.*, 2009) but because such models are data hungry (Nicholson *et al.*, 2006; Pöyry *et al.*, 2008; Araújo, 2009) their use is not appropriate for species which lack such detail (e.g. rare or threatened species). Furthermore, process-based models could be argued to be at a distinct disadvantage in terms of accessibility and use-ability compared to the more pragmatic SDMs (Araújo, 2009). Therefore, the concept of modelling using precise species trait data which represents a measure of fitness is enticing but clearly limited in application. However, developing community level traits, may help assess the response of the community to environmental change as well as infer the response of rare species (Elith *et al.*, 2006), as models are based on trait occurrence not species occurrence (Ferrier and Guisan, 2006).

While traits may provide ecological realism, SDMs have generally struggled with the community aspect of species models. Given the complexities of ecosystems, this last point is hardly surprising. Attempts have been made using ensemble modelling, reconstructing communities from individual species models (Ferrier and Guisan, 2006). Ensemble community modelling is based on the ecological tacit that species do not exist in isolation, therefore we would expect interactions to be mediated by community dynamics. For example, in evolutionary biology the constraints of inter-specific competition can modify a species response across its range (Lavergne *et al.*, 2010). Lavergne *et al*. (2010) suggest that competition, in theory, could modify a species response to climate change and a handful of studies support the theory (Davis *et al.*, 1998; Bak and Meesters, 1999; Grant and Grant, 2006; de Mazancourt *et al.,* 2008; Johansson, 2008). Essentially, the rate of shift or decline is likely to be mediated by inter-specific competition and suggests that modelling of trailing and leading edges should be made in a community, rather than individual species, context. Further, the link between climate and species response may be weaker than previously realised; bird species for example, appear to have their response [to climate] mediated by biotic interactions (Faisal *et al.*, 2010), meaning that modelling of community structure may be a valuable tool in predictive modelling. Modelling using ecological realities is critical, particularly if the model is applied to highlight rare species conservation needs (Hernández *et al.*, 2006; Nicholson *et al.*, 2006) and consequently used by conservation managers to help implement legislation changes or protect areas of importance (Austin, 2002; Nicholson *et al.*, 2006; Hof *et al.*, 2011). The spatial and temporal scale used in a model coupled with ecological realism is essential in order to provide models (projections) (Nicholson *et al.*, 2006; Ficetola *et al.*, 2010) which inform conservation decisions. Accounting for biotic interactions remains a challenge (Elith and Leathwick, 2009) and linking species traits to spatial habitat data at a relevant scale, as well as understanding the response of a population or community throughout the area of occupancy, will be an important tool in conservation planning.

1.2.4 Species distribution models and conservation planning.

A cornerstone of conservation is the use of protected areas (Rodrigues *et al.*, 2004). Decision making in these reserves is a process fraught with conflict and achieving a balance between stakeholders and biodiversity aims is difficult. Recommendations made by conservationists are sometimes informed by SDMs using limited data (Loiselle *et al.*, 2003). However, while pragmatic, limited data has the potential to have profound effects on conservation outcomes and may often lead to omission (species is thought to be absent) or commission errors (species is considered present in a protected area when it is absent) (Loiselle *et al.*, 2003). Thus, model limitations can provide erroneous decisions, particularly for rare species, through poor predictions of the extent of occurrence. In planning or managing protected areas, these ‘coarse’ models may give rise to commission errors, which can ultimately either ineffectively target resources and/or implement unnecessary management practices (Loiselle *et al.*, 2003; Rodrigues *et al.*, 2006; Rondinini *et al.*, 2006).

Additionally, management strategies in protected areas are often developed based on environmental stasis with minimal consideration for climatic shifts or changing landscapes (Lee and Jetz, 2008; Hole *et al.*, 2011). Inappropriate scale is a problem for decision makers and planning. Reserve networks are sensitive to spatial scale; conservation planning is often carried out at the site level (Platts *et al.*, 2010), however, very few studies which utilise SDM as a planning tool consider the spatial scale. The lack of forward planning, isolation from the planning framework of the reserve system (Hole *et al.*, 2011) and susceptibility to edge effects for relatively immobile species condemns the temporal usefulness of static reserve systems as a buffer against climate (Lee and Jetz, 2008). Reserve networks are also affected by further metrics of which landscape measures are important and as such should constitute part of the modelling process (Lippitt *et al.*, 2008); calls for systematic approaches to mapping ecosystem services are apparent in the literature (Menon *et al.*, 2001; Carpenter *et al.*, 2006; Lippitt *et al.*, 2008; Swetnam *et al.*, 2011). Inclusion of land-use measures into species distribution models is problematic, partially due to the complexity of the human-landscape relationship (Carpenter *et al.*, 2006; Rogers *et al.*, 2010) and partially because in order to provide long-term and relevant projections, the land-use model implemented really needs to be dynamic (Ficetola *et al.*, 2010). Part of the issue of complexity is that land-use is driven by a range of socio-economic factors, which themselves are driven by significant environmental cues such as climate (Falcucci *et al.,*2006).

1.3 Amphibians

1.3.1 Amphibians and Species Distribution Models

To investigate models, it appears prudent to study those groups of animals which display vulnerability to environmental conditions, show high degrees of endemism and face ongoing significant extinction events. As amphibians (composed of three orders; Anura (frogs), Caudata (newts and salamanders) and Gymnophiona (caecilians)) rely heavily on surrounding environmental conditions they are thought to be more likely to be highly sensitive to climate change (Blaustein and Belden, 2003; Cushman, 2006; Buckley and Jetz, 2007) and as a vertebrate group are already undergoing a significant extinction event (Stuart *et al.*, 2004; Wake and Vredenburg, 2008; Dixo *et al.*, 2009). In part, the susceptibility of amphibian lineages to extinction has been attributed to a generally poor dispersal ability and narrow environmental tolerances coupled with underlying primary drivers for extinction (e.g. habitat loss and fragmentation, invasive species etc) (Dixo *et al.*, 2009). However, some authors question poor dispersal ability (Smith and Green, 2005) and narrow environmental tolerance (Navas, 1996; Scheffers *et al.*, 2013b) and suggest that functional traits broaden amphibian response to the environment providing there is suitable habitat available (Vallan, 2000; Becker *et al.*, 2010; Scheffers *et al.*, 2013a). Regardless, the synergy between primary drivers and threats such as climate change and the presence of novel emerging pathogens is of concern (Beebee and Griffiths, 2005; Pounds *et al.*, 2006). The cumulative effect of synergistic relationships is likely to be the main agent driving an estimated 30% of amphibians towards extinction (Hof *et al.*, 2011). According to the coarse scale findings of Foden *et al*. (2007), of the 6,222 extant amphibian species, 52% (3,217) are potentially susceptible to climate change. While there have been many studies on vertebrate responses to climate change, very few studies have been published for amphibians despite the clear aims from the IUCN's Amphibian Conservation Action Plan (Zippel and Mendelson III, 2008).

Amphibians embrace many of the attributes that make fine-scale modelling problematic. For many rare amphibian species distribution data and ranges are often inadequately defined (Lawler *et al.*, 2010) leading to poor modelling performance. Species-specific ecology is also typically poorly understood but generally amphibians are considered to be constrained by stringent water requirements and thermal dependency (Buckley and Jetz, 2007). For ectotherms as a rule, the suggestion is, that in order to colonise high elevations, temperature is a limiting factor but may not constrain diversity, as thermal adaptation is common in diverse taxa (Navas, 2006). Therefore, the upper limits of regional amphibian richness may be set by a single environmental predictor, but it is unlikely to exclusively determine diversity (Buckley and Jetz, 2007). Indeed, amphibians seemingly maintain patterns of behaviour and ecology but shift physiology to adapt to lower temperatures (Navas, 2006), retaining signals within a population of historic events that produced current species distributions (Zeisset and Beebee, 2008). Within region diversity has been shown to be driven jointly by water and temperature (Buckley and Jetz, 2007) and other variables may also play a strongly selective role in species richness (i.e. ultra-violet radiation, particularly in high altitudinal regions) (Carey *et al.*, 2001; Middleton *et al.*, 2001; Navas, 2006), suggesting that eco-physiological constraints, other than temperature, determine broad-scale responses by amphibians. Thus, historical colonisation of tropical montane systems by amphibians appears to contrast with other ectotherms.

Amphibians are susceptible to landscape features beyond a simple function of vegetation characteristics and broad climatic clines, demonstrated in coarse-grained bioclimatic models. The impact of anthropogenic modifications to landscapes, such as roads, fragmentation and agricultural practices (Cushman, 2006), precludes colonisation or dispersal to adjacent areas (Ficetola *et al.*, 2010) regardless of suitability of habitat. This susceptibility is further compounded by traits; amphibian species which exhibit low mobility and high philopatry to sites (Zeisset and Beebee, 2008) tend to be strongly associated with specific vegetation classes or topographic characteristics. The strong association between amphibians and the environment ultimately means, whether through reduced connectivity between populations (gene flow) or post-metamorphic dispersal, that anthropogenic land-use or disturbance regimes will influence the persistence of amphibian populations (Cushman, 2006; Bastazini *et al.*, 2007; Ficetola *et al.*, 2010).

1.3.2 Malagasy amphibians and important habitats

For all species facing climate change, there are three options: shift range, adapt or become extinct (Foden *et al.*, 2008; Anderson *et al.*, 2009). While relatively simplistic, coarse-grained models may provide useable projections for wide-spread, mobile, generalist species, the issue of scale and accuracy in climate change modelling becomes more apparent when regions with unique micro-climates are considered. Tropical montane systems normally vary significantly in their microclimates due to the variability of topography, ultimately meaning that montane species are often specialists (Ricketts *et al.*, 2005) as they encounter range-limiting climatic conditions (Hannah *et al*., 2002). These ecotypes may therefore be constrained in their ability to adapt to climate change; however, coarse grained models do not demonstrate the response of specific ecosystems or even species (Trivedi *et al.*, 2008) which results in erroneous predictions particularly for small and vulnerable ecosystems such as tropical montane. This problem of predictability has been further compounded by simplistic range-shift theories (movement of a species up or down a slope according to temperature), whereas shifts in habitat zones are much more complex and incorporate dependency on precipitation and are orientated on a species' individual requirements (Halpin, 1997; Bush, 2002).

Tropical montane systems are an important habitat for amphibians: approximately 2714 species (c. 47% of all known amphibians) are found in tropical montane habitats and 75% of declines in montane systems are considered enigmatic (Pounds *et al.*, 1997; Stuart *et al.*, 2004). The vulnerability of most tropical montane assemblages to climate change effects has not been well documented (Rull and Vegas-Vilarrubia, 2006), despite these regions exhibiting typically high levels of local endemism (Ricketts *et al.*, 2005; Ledo *et al*., 2009) and the expectation that most climate-driven extinctions are likely to occur in areas with high degrees of species specialism (Raxworthy *et al.*, 2008). Additionally, tropical montane forest is a fragile ecosystem under pressure from anthropogenic disturbance (Ledo *et al*., 2009). Vegetation community composition is shifting in some tropical montane environments, moving away from an ecosystem dominated by species adapted to humid conditions to those that are more tolerant of drier climates (Ledo *et al.*, 2009). Further, tree species diversity/species richness and proximity to tracks and pathways is negatively correlated suggesting that a level of anthropogenic disturbance plays a role in community's ecological structure (Ledo *et al.*, 2009).

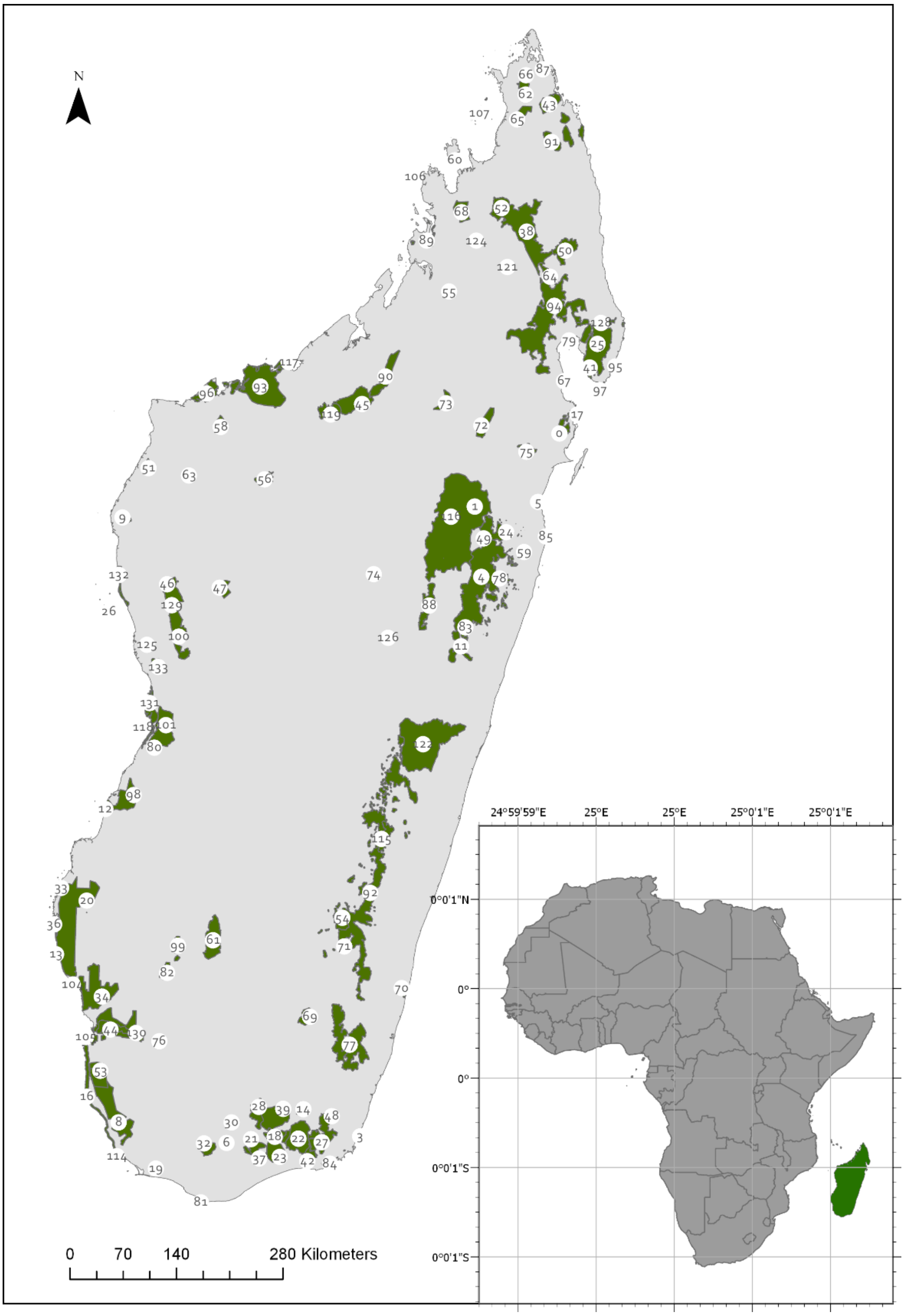
Amphibian research and research within specific ecosystems appears to be biased, with predominately more studies being conducted in the new world and South-east Asia (Gardner *et al.*, 2007, 2010). Despite the importance of amphibian diversity of many sub-Saharan regions, this area suffers from a lack of studies (Gardner *et al.*, 2007). This lack of study is alarming as sub-Saharan tropical montane systems account for nearly 50% for all known species in the region, of which 70% are endemic (Poynton, 1999). In the Afrotropical realm, 43% of tropical montane species are threatened (Andreone *et al.*, 2008a). Despite the significant contribution of tropical montane systems to amphibian diversity and the increased likelihood of extinction of amphibians through constrained response to climate scenarios, surprisingly little focus has been placed on this important ecosystem. Aside from parts of the Americas, regions where climate change is projected to have a high impact include sub-Saharan tropical Africa; this region is also expected to see notable levels of land-use change (Hof *et al.*, 2011). Overall, there appears to be little literature addressing the effect of climate and amphibian species distribution in tropical montane ecosystems in sub-Saharan Africa and limited indications of the impact of habitat disturbance/land-use (Poynton, 1999). Of specific interest to this study are those tropical montane systems found in the Afrotropical realm explicitly in Madagascar.

Next page: *Fig. 2. Diversity of Malagasy amphibians. Clockwise from top right: rainforest habitat at Betampona (Michael Bungard), Heterixalus punctatus (Daniel Austin), Mantella baroni (Daniel Austin), Heterixalus alboguttatus (Daniel Austin), Gephyromantis ambohitra (Daniel Austin), Mantella crocea (Michael Bungard), Heterixalus madagascariensis (Daniel Austin), Mantella aurantiaca (Michael Bungard). Centre: Mantella laevigata (Michael Bungard).*

Madagascar is important for amphibians, specifically order Anura (frogs), due to the degree of diversity (Fig. 2) and endemism exhibited by the taxa (Vieites *et al.*, 2009) and has escaped large-scale, recent amphibian extinctions such as those reported in many other areas of the world (Andreone *et al.*, 2005; Andreone *et al.*, 2008b). While Madagascar's amphibian fauna does not appear to be presently threatened by novel pathogens (e.g. *Batrachochytrium dendrobatidis,* Bd) (however, see Kolby, 2014), they are imperilled by heavy anthropogenic pressure (Busch *et al.*, 2012) and consequent habitat fragmentation (Vallan, 2000; Andreone *et al.*, 2005). The island has been subjected to severe loss of forest habitat that previously covered much of the eastern slopes of the country as well as the central highlands (Ganzhorn *et al.*, 2001; Harper *et al.*, 2007); much of what now remains is isolated, relict forest habitat (Durkin *et al.*, 2011). The eastern rainforest slopes, which have partially survived the onslaught of deforestation, also contain the greatest amphibian diversity (Andreone *et al.*, 2005). However, complex spatial patterns of endemism exist throughout all taxonomic groups in Madagascar, and this complexity challenges the creation of protected areas and planning priorities (Kremen *et al.*, 2008). Overall, questions have been raised regarding the current reserve network's (Fig. 3) ability to protect the island's remaining biodiversity (Ganzhorn *et al.*, 2001; Hannah *et al.*, 2008; Rabearivony and Thorstrom, 2010), specifically amphibians (Andreone *et al.*, 2005). Further, considering that more than 80% of Madagascar's remaining forest mosaic is adjacent to a predominately rural human population (Irwin *et al.*, 2010) and that amphibians are particularly susceptible to edge effects (Lehtinen *et al.*, 2003; Irwin *et al.*, 2010), it is surprising that many of Madagascar's amphibian species manage to persist. It could be argued, somewhat fatalistically, that extinction of some species appears to be inevitable (Andreone *et al.*, 2008b; Rogers *et al.*, 2010).

Regional warming trends for Madagascar have not been widely explored and despite the potential vulnerability of montane assemblages further scientific validation of climate change impact does not appear to be forthcoming (Raxworthy *et al.*, 2008). Furthermore, species in montane ecosystems may experience elevation-dependent warming, where increasing altitude amplifies the rate of warming (Pepin *et al*., 2015). As the species assemblages in certain regions of Madagascar's highlands contain multiple endangered and critically endangered frog species (Andreone *et al*., 2005; Glaw and Vences, 2007), there is a need to understand the relationship between amphibians and their immediate environment and how that relationship can potentially change if climatic shifts occur. While the current system of protected zones encompasses 82% of threatened amphibian species (Andreone *et al.*, 2005) there are no indications how those zones will buffer species against climatic shifts.

Fig. 3. Terrestrial protected areas (dark green) of Madagascar. Numbered circles refer to protected areas; names are given in Table S1. Spatial data source: Protected Planet: The world database on protected areas (WDPA) (UNEP-WCMC and IUCN, 2018). Inset map shows Madagascar's (dark green) geographic position to Africa.



1.4 Summary of thesis aims and structure

The thesis aims to explore a mechanism whereby rare or threatened species in restricted habitats can be included in spatial CCVA. Specifically, it investigates whether species functional traits can act as a viable proxy for those species with few associated data. I also examine the importance of including habitat variables for amphibian-centric models. The thesis then investigates the potential impacts of climate change on threatened Malagasy amphibians, with a focus on the protected area network.

Chapter 2 describes a hybrid trait-SDM framework (Trait Distribution Models) and its application to CCVA. The framework was specifically developed to capture species with few occurrences. The framework uses a mixture of ordination and K-means clustering followed by species distribution modelling to show the spatial response of functional traits to climate change. Data for this chapter is freely available (Bungard, 2019) and is stored in the Knowledge Network for Biocomplexity.

Chapter 3 focuses on the environmental variables used in a trait distribution model and whether incorporating habitat variables improves model performance. A null model is used to explore the relationship between three model variants: climate-only, habitat-only and climate+habitat. Climate-only models are then assessed for spatial over-prediction and whether over-prediction is related to the specialism of a trait complex (measured by niche breadth). Response curves from the best performing models are used to examine the relationship between functional traits and the environment. I then discuss the implications of responses in context of habitat management.

Chapter 4 uses the TDM framework developed in Chapters 2 and 3, to investigate the climate sensitivity of threatened species and whether the Malagasy protected area network can potentially encompass threatened species in the future, according to two end-of-century (2085) climate scenarios.

Chapter 5 draws together all previous chapters in defining the contribution and impact of the thesis. I also discuss areas for further development and future research.

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1.6 Supplementary

Table S1. Identifiers and Madagascar protected areas in Figure 1.

Identifier	Protected area	Identifier	Protected area
0	Mananara-Nord	67	Andreba
1	Alaotra	68	Manongarivo
2	Antisakivolo	69	Kalambatritra
3	Ambatoatsinanana	70	Manombo
4	Zahamena Ankeniheny	71	Pic d'Ivohibe
5	Tampolo	72	Marotandrano
6	Vohimena	73	Tampoketsa Analamaitso
7	Seranambe	74	Ambohitantely
8	Parc national Tsimanampesotse	75	Ambatovaky
9	Lac Kinkony	76	Bezaha Mahafaly
10	Zone Humide de Mandrozo	77	Midongy du sud
11	Analamazoatra	78	Mangerivola
12	Complexe des lacs Ambondro et Sirave (CLAS)	79	Nosy Mangabe
13	Soariake	80	Andranomena
14	Beteny	81	Cap Sainte-Marie
15	Soariake	82	Zombitse-Vohibasia
16	Littoral Sud Toliara	83	Mantadia
17	Nosy Atafana	84	Ambatotsirongorongo
18	Ifotaka	85	Analalava
19	Vohidefo	86	Mandena
20	Mikea	87	Montagne des FranÃ§ais
21	Angavo	88	Anjozorobe Angavo
22	Behara-Tranomaro	89	Sahamalaza
23	Sud-Ouest Ifotaky	90	Bongolava
24	Zahamena	91	Daraina
25	Masoala	92	Fandrina Vondrozo
26	Future AMP Barren	93	Mahavavy Kinkony
27	Corridor entre Parcelles I et II d'Andohahela	94	Makira
28	Tirimena-Voaimongotse	95	Tanjona
29	Ambia	96	Baie de Baly
30	Vohipary	97	Ambodilaitry Masoala
31	Beompa	98	Kirindy Mitea
32	Marobasia	99	Vohibasia
33	Tsinjoriake	100	Tsingy de Bemaraha
34	Ranobe PK 32	101	Menabe
35	Extension ala maiky Ankodida Tsimelahy	102	Maintimbato
36	Manjaboaka	103	Velondriake

37	Extension ala maiky Ampamalora	104	Fimihara
38	Corridor Marojejy Tsaratanana	105	Tahosoa
39	Ekintso	106	Ankivonjy
40	Extension ala maiky Ankodida Tranomaro	107	Ankarea
41	Tampolo	108	Nosy Ve
42	Ankodida	109	Analanjahana
43	Analamerana	110	Aniribe
44	Onilahy	111	Tampolo
45	Ankarafantsika	112	Imorona
46	Tsingy de Bemaraha	113	Vohitralanana
47	Ambohijanahary	114	Ambohibola
48	Andohahela	115	Ranomafana
49	Zahamena	116	Le Lac Alaotra: les zones humides et basin
50	Marojejy	117	Site Bioculturel d'Antrema
51	Bemarivo	118	Zones humides de Bedo
52	Tsaratanana	119	Zones Humides Ankarafantsika (CLSA)
53	Tsimanampetsotsa	120	Marais de Torotorofotsy avec leurs bassins versants
54	Andringitra	121	Lac Sofia
55	Bora	122	Riviere Nosivolo et affluents
56	Kasijy	123	Barriere de Corail Nosy Ve Androka
57	Amboditangena	124	Complexe des Zones Humides de Bemanevika
58	Tsingy de Namoroka	125	Complexe des lacs de Manambolomaty
59	Betampona	126	Parc de Tsarasaotra
60	Lokobe	127	Zones Humides de Sahamalaza
61	Isalo	128	Rainforests of the Atsinanana
62	Montagne d'Ambre	129	Tsingy de Bemaraha Strict Nature Reserve
63	Maningoza	130	Zones humides de l'Onilahy
64	Anjanaharibe-Sud	131	Mangroves de Tsiribihina
65	Ankarana	132	Iles Barren
66	Foret d'Ambre	133	Zones humides d'Ambondrobe

Chapter 2. Developing a trait-based spatial vulnerability tool to assess extinction risk for Malagasy amphibians under climate change

Preface

Although climate change vulnerability assessment is a useful tool in spatially assessing the response of species to future climatic shifts, rare or threatened species present us with a paradox. Such species are the most in need of assessment yet lack enough data to implement species distribution models (SDMs). Therefore, for such species there is no detail of changes of range size under predicted climate change. There is a growing call for climate change vulnerability to be comprehensively included into IUCN Red List assessments (Foden *et al.*, 2013; Foden and Young, 2016; IUCN SSC Standards and Petitions Subcommittee, 2017) but the rare species paradox creates a substantial hurdle to inclusion. In addition to aiding Red List assessments, the ability to target valuable and limited conservation resources through details in range changes, would be an asset. This chapter presents a novel framework which aims to address the paradox by analysing the response of species traits to the environment, thereby capturing influential aspects of ecology and life history and producing the spatially explicit outputs valuable for conservation planning.

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2.1 Abstract

The degree to which species can shift their distribution ranges in response to climate change is a key determinant of their survival. Anticipating such shifts is a priority for conservation, especially for species already vulnerable to other threats. Because many such species have narrow ranges or incomplete distribution data, assessment of their climate change vulnerability is often omitted or relies on trait-based approaches which do not predict changes in suitable climate space. We present a novel Trait-Distribution Modelling (TDM) framework which combines qualitative trait information for species with data on their spatial and climatic distributions, to assess climate change vulnerability across all species. Applied to all 248 Malagasy amphibians, we found that functional traits for threatened species (IUCN Red List) clustered into three complexes. The distributions of these complexes were climate sensitive, particularly correlated with the length and severity of the dry season. Depending on the complex and the Representative Concentration Pathway (RCP), we project a 53-98% reduction in suitable climate space for Malagasy amphibians by 2085. General trends demonstrated an upslope shift in climatic suitability. However, taxa that are resilient to climate change tend to concentrate in the mid-altitudinal range and as such, these areas are priorities for conservation actions to connect habitat pathways. The TDM framework presented here on Malagasy amphibians has much wider potential use in assessing the climate vulnerability of other rare and threatened species groups, both in Madagascar and globally.

Keywords: Madagascar, CCVA, threatened species, data paucity, restricted habitats

2.2 Main

2.2.1 Introduction

Rapid, anthropogenically-induced climate change is impacting on species ranges globally (Tingley *et al.*, 2009; Allen *et al.*, 2010; Chen *et al.*, 2011; Scheffers *et al.*, 2016; Sofaer *et al.*, 2018). In combination with land-use change, invasive species and pathogens, climate change is likely to become a leading driver of future biodiversity losses (Pacifici *et al.*, 2015). To address the urgent need for assessments of climate change vulnerability for large numbers of species, Species Distribution Models (SDMs) or Trait-Based Assessments (TBAs) (Pacifici *et al.*, 2015) are often selected over a more resource-intensive mechanistic approach (Foden *et al.*, 2018). SDMs correlate species' occurrences with climatic gradients, and then use this to project species' available climate space into the future (Summers *et al.*, 2012; Willis *et al.*, 2015). However, this procedure disproportionally omits rare species or those with few collection records, to the extent that a large proportion of species listed in Threatened categories on the IUCN Red List are ineligible for large-scale SDM approaches (Platts *et al.*, 2014). Alternatively, TBAs consider life history, ecological and genetic traits (termed functional or species traits) as indicators of a species' sensitivity and adaptability under climate change (Willis *et al.*, 2015). TBAs accommodate rare species through expert assessments of traits (scoring of traits does not rely on minimum numbers of occurrence records), but they provide no information on potential range changes in response to changing climate. Because of the respective challenges associated with both approaches, spatially-explicit Climate Change Vulnerability Assessments (CCVA) are lacking for many of the world's most unique and threatened taxa or species assemblages.

Malagasy amphibians (order Anura, frogs) exemplify the challenges associated with conducting CCVA for threatened taxa. Their biphasic lifestyle (larval/tadpole stage and distinct adult form) makes them particularly vulnerable to changes in both water availability and temperature (Buckley and Jetz, 2007; Becker *et al.*, 2010), while high levels of speciation and philopatry in heterogeneous landscapes (Buckley and Jetz, 2007; Zeisset and Beebee, 2008) make available records highly restricted in number and extent. Of the 248 amphibian species found in Madagascar, two-thirds (166 species) have insufficient data for SDM application (n < 10 on a 1 km grid), of which 39% (65 species) are threatened with extinction (Vulnerable, Endangered or Critically Endangered on the IUCN Red List). We overcome this challenge for Malagasy amphibians using a new hybrid tool that combines trait- and distribution-based methodologies (Fig. 1), here called a Trait Distribution Model (TDM), which allows for a taxon-wide CCVA that draws on data from all 248 species.

Our methodology produces latent trait variables that in part describe a species' niche and can be assumed to reflect the adaptive response of traits to the environment (Thuiller *et al.*, 2004). Under assembly rules (Keddy, 1992) the environment acts as a filter, removing those species with traits unsuited for a set of environmental conditions. Two datasets are required, a species pool and a matrix of traits per species and is concurrent with the 'assemble first, predict later' approach suggested by Ferrier and Guisan (2006). To create the matrix of traits, we analysed peer-reviewed literature, field guides and online resources such as the IUCN Red List for accounts of all 248 species of Malagasy amphibian and recorded six categorical traits (Table 1). Four traits corresponded directly to life history traits (larval deposition site and egg deposition site (following Duellman and Trueb, 1994; Glaw and Vences, 2007), preferred adult microhabitat (Crump, 2015) and body size). Whilst we searched the literature extensively, elusive traits such as voltinism and clutch size may be required to further distinguish groups. To mitigate for missing traits, we chose two proxy traits for specialisation (altitudinal range and habitat breadth (McPherson and Jetz, 2007; Böhm *et al.*, 2016; Yu *et al.*, 2017)). Traits are often intercorrelated because individual traits are unlikely to have evolved in isolation (Verberk *et al*., 2013), so detecting clear links between environmental stressors and individual traits is difficult (Verberk *et* al., 2013; Mbaka *et al*., 2015). We therefore derived two trait variables through categorical ordination (Table 2): the first variable described microhabitat and reproductive techniques and accounted for most of the variance within the dataset (49.767%). Variable two (28.302% of variance) was described by habitat adaptability and altitudinal range of a species; this dimension defines a species' ability to be a specialist or generalist. Our methodology allows multiple traits to be combined (Cadotte *et al.*, 2015) and produces a qualitative measure of trait interaction.

Fig. 1. Trait Distribution Modelling (TDM) framework for assessing climate change vulnerability of species. By combining qualitative species accounts with quantitative spatial data on distribution and climate, for all species in a group, the framework provides the first spatial assessments of climate change vulnerability of rare and threatened amphibians in Madagascar.

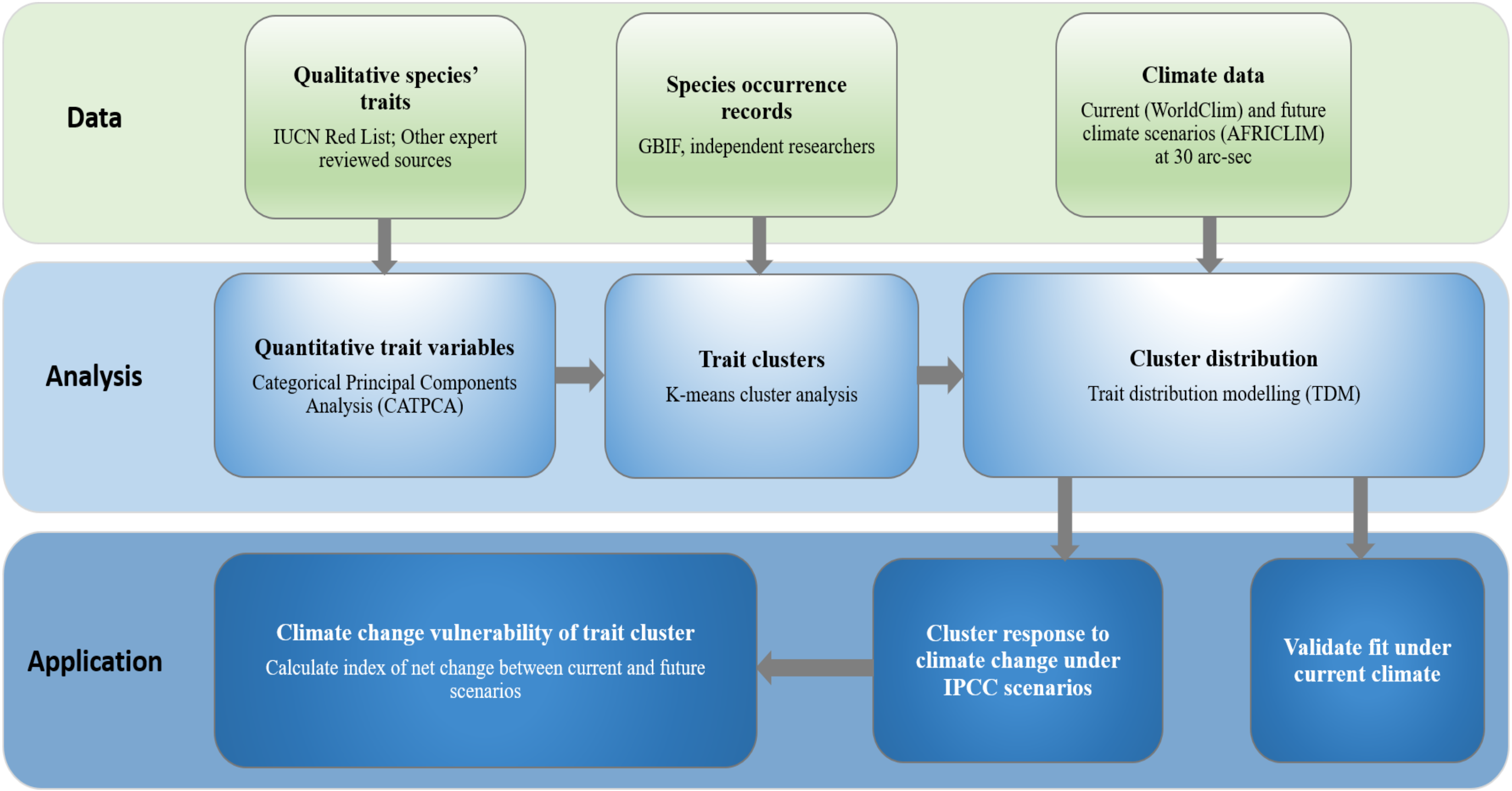


Table 1. Summary of species traits and their descriptions used for categorising Malagasy amphibians.

Trait	**Trait categories**	**Description**
Larvae deposition site	Lentic water bodies	Any pools, ponds or other still water
	Lotic water	Any running water
	Nest development	Tadpole development within nest, no free-swimming tadpole stage
	Direct development	No tadpole stage
	Phytotelmata	Tadpoles develop in permanent or temporary pools in tree hollows, leaf axils or similar arboreal water bodies
	Unknown	Larval deposition is unknown
Egg deposition site	Lentic water bodies	Any pools (other than arboreal), ponds or other still water
	Lotic water bodies	Any running water
	Phytotelmata	Eggs laid in water held within tree hollows or leaf axils
	Terrestrial	Eggs laid on the ground
	Arboreal	Egg clutches attached to foliage
	Unknown	Egg deposition is unknown
Preferred adult microhabitat	Aquatic	Typically found in water, either lentic or lotic
	Semi-aquatic	As above but demonstrate some terrestrial behaviour
	Fossorial	Adapted for digging/life below ground
	Terrestrial	Typically found on land e.g. forest floor
	Semi-arboreal	Adults typically found up to 2 m above ground
	Arboreal	Adults typically found > 2 m above ground
	Unknown	Adult microhabitat unknown
Size	Snout-vent length	Average of quoted male/female snout-vent length (mm)
Habitat adaptability	14 broad habitat descriptors	Swamp, heath & moor, primary rainforest, secondary rainforest, bamboo forest, canyons & rock outcrops, dry forest, dry degraded, urban/roadside, savannah & grassland, open habitat (not agricultural), transitional forest, plantations, open agriculture (e.g. rice paddies)
Altitudinal range		Difference in metres between minimum and maximum of species altitude range

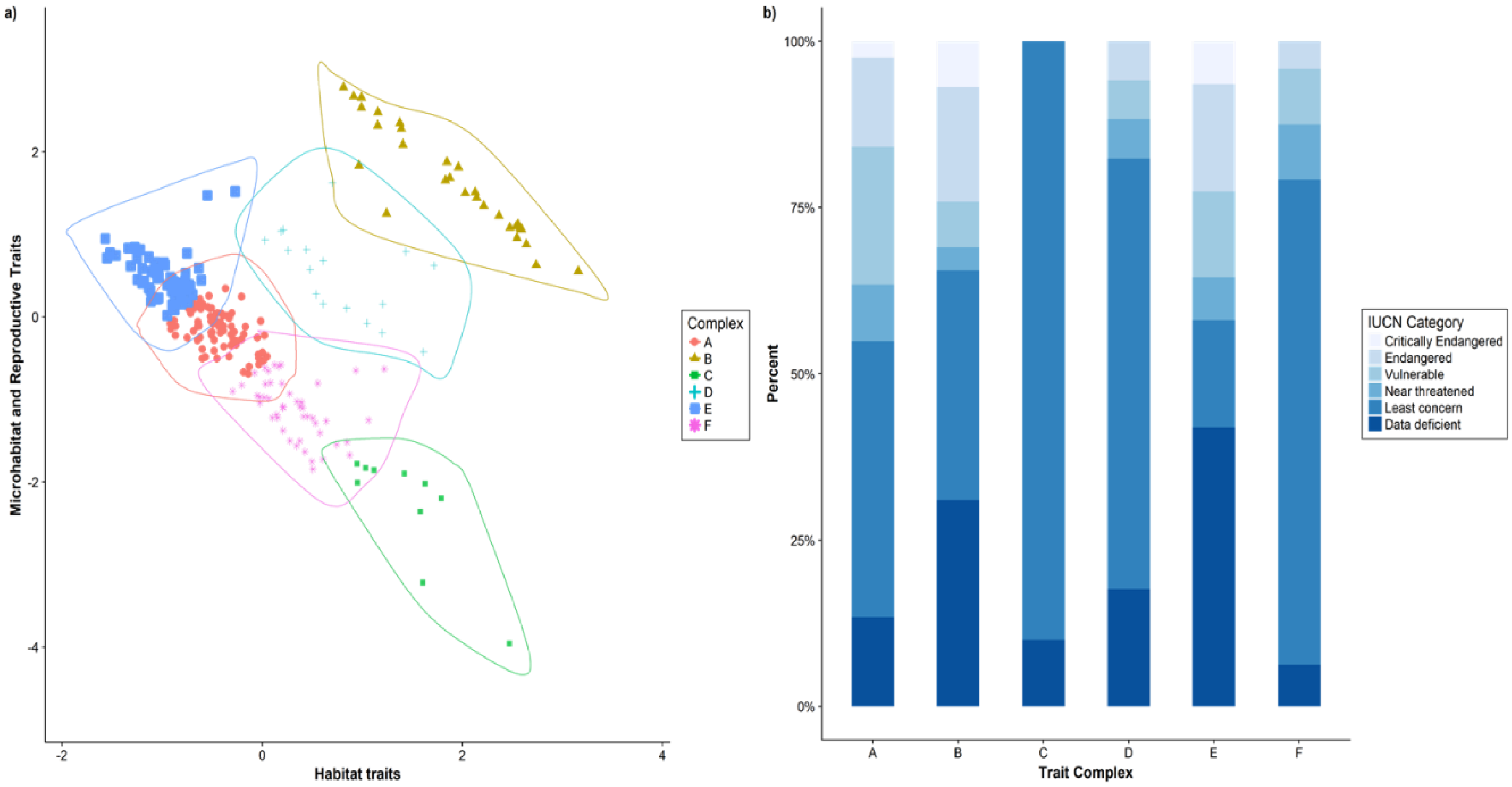
Table 2. Weightings (variance accounted for) of trait variables for each dimension in Categorical Principal Components Analysis (CATPCA). Trait variables whose centroid coordinate scores contributed greatly to the interpretation of the final dimension are highlighted in bold. Eigen values and % of variance for each dimension are given.

Trait variable	**Dimension**	
	1	**2**
Egg deposition site	**0.904**	0.053
Larvae deposition site	**0.869**	0.054
Size (snout-vent-length)	0.152	0.307
Altitudinal range	0.235	**0.715**
Preferred adult microhabitat	**0.783**	0.053
Habitat adaptability	0.044	**0.516**
Eigen value	2.986	1.698
% of variance	49.767	28.302
Cumulative variance	49.767	76.069

2.2.2 Results and discussion

Using K-means clustering (Valle and Silva, 2006), we identified six trait complexes that are independent of phylogenetic relationships (Supplementary Table S1). The removal of taxonomic linkage is important because rare species often exhibit specific traits not found elsewhere within the genus. Thus, trait reliance ("borrowing strength" from more common related species; Pollock *et al*., 2012) can lead to false emphasis on the relative importance of a functional trait, compromising the ability of taxonomic groupings to assess climate change vulnerability. We found that 88% of threatened species cluster into three of the six complexes (A, B and E; Fig. 2). Complex A represented predominately adults found in low vegetation/terrestrial with some habitat flexibility (understorey species); complex B represented arboreal species with high reliance on vegetation for both microhabitat and breeding mechanisms (reliance on phytotelmata for both egg and tadpole deposition); complex E represented terrestrial to low vegetation (< 2 m) adults, habitat specialists. Other complexes (C, D and F) represented habitat generalists, where complex C represented generalists with large range sizes.

Fig. 2. The distribution of Malagasy amphibians across trait complexes and the spread of IUCN categories within each complex. ***a)*** *Species cluster according to their trait combinations: positive values on the y-axis refer to increasing arboreal preferences whilst negative values refer to increasing aquatic life history; on the x-axis, positive values of habitat traits refer to generalists and negative values, habitat specialists. Six complexes are identified, three of which (A, B and E, bold) contain 88% of all threatened Malagasy amphibians, as shown in (****b****).*



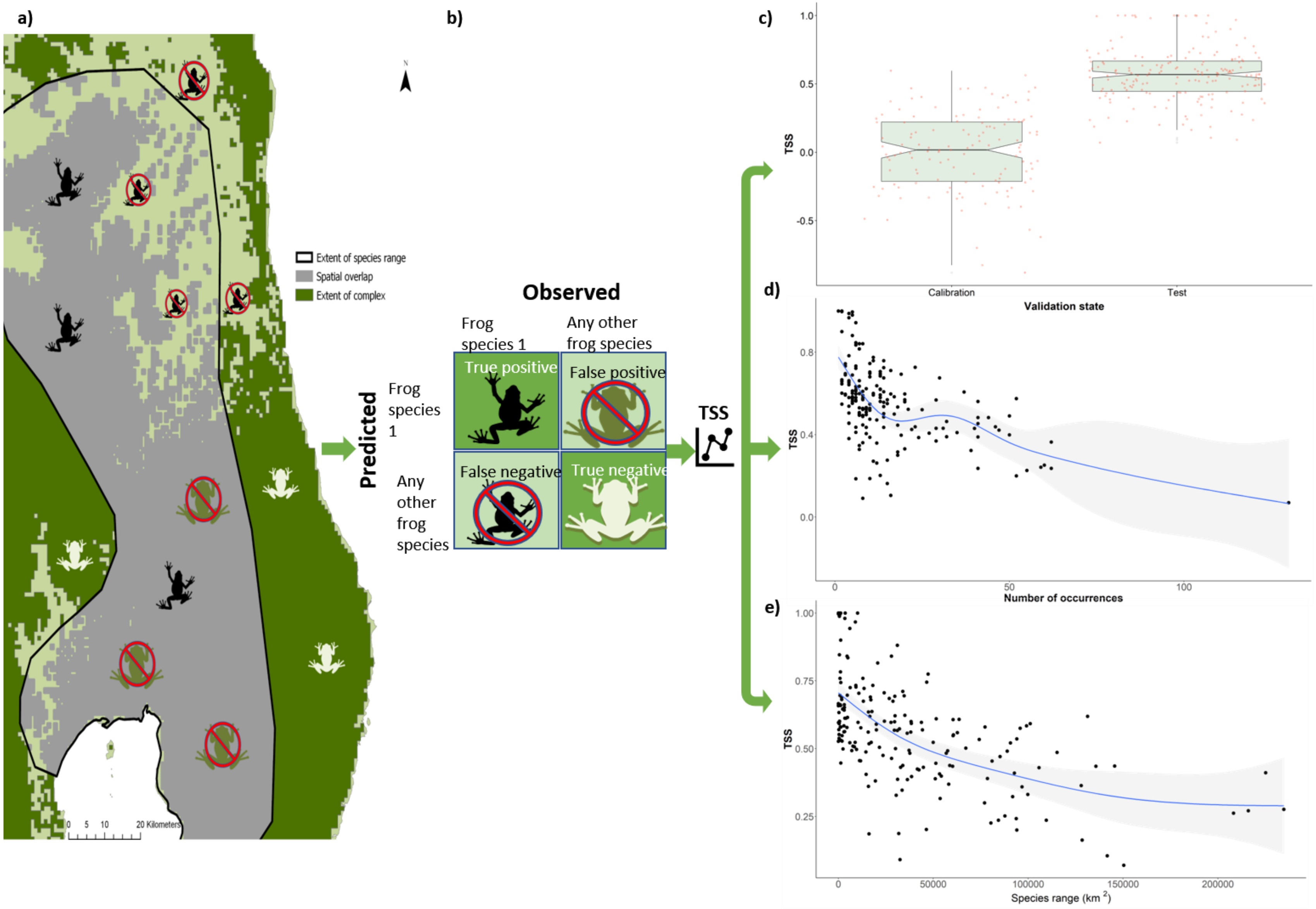
We then mapped the spatial distribution of each trait complex and quantified the sensitivity of these distributions to climate. Because the historic biotic-environment interactions linked to climatic variability (Wisz *et al.*, 2013) have been selected through evolutionary processes (Keddy, 1992; Ferrier and Guisan, 2006), traits relating to these interactions can help to explain the mechanisms through which a species exploits its specific range; the extant traits being most suited to the environmental range of the species (Keddy, 1992). We obtained trait distribution data by linking 2,990 species distribution records with the respective species' traits, and then pooling these records according to the composite traits that define each complex. Relationships with climate were assessed along four climatic gradients (Supplementary Table S2), capturing spatial and seasonal variation in temperature and precipitation. Model performance was assessed by both Area Under the Curve (AUC) and True Skills Statistic (TSS) and all models performed well (Table 3). A cut-off of AUC > 0.8 (Landis and Koch, 1977) and TSS > 0.4 (Liu *et al.*, 2005) were selected to determine whether models were useful or not. Complexes A, B, and E, which contained rare species perform far better than either C or F, both of which are composed of generalists/wide-ranging species.

Table 3. Performance of TDM for trait complexes (A-F). Area Under the Receiver Operating Characteristic Curve (AUC) and True Skills Statistic (TSS) are reported. Models with good accuracy (for AUC > 0.8, TSS > 0.4) are highlighted in bold.

Trait complex	**AUC**	**Standard deviation**	**TSS**
A	**0.811**	0.020	**0.522**
B	**0.848**	0.017	**0.570**
C	0.753	0.041	**0.445**
D	**0.882**	0.019	**0.635**
E	**0.854**	0.047	**0.583**
F	0.760	0.024	**0.425**

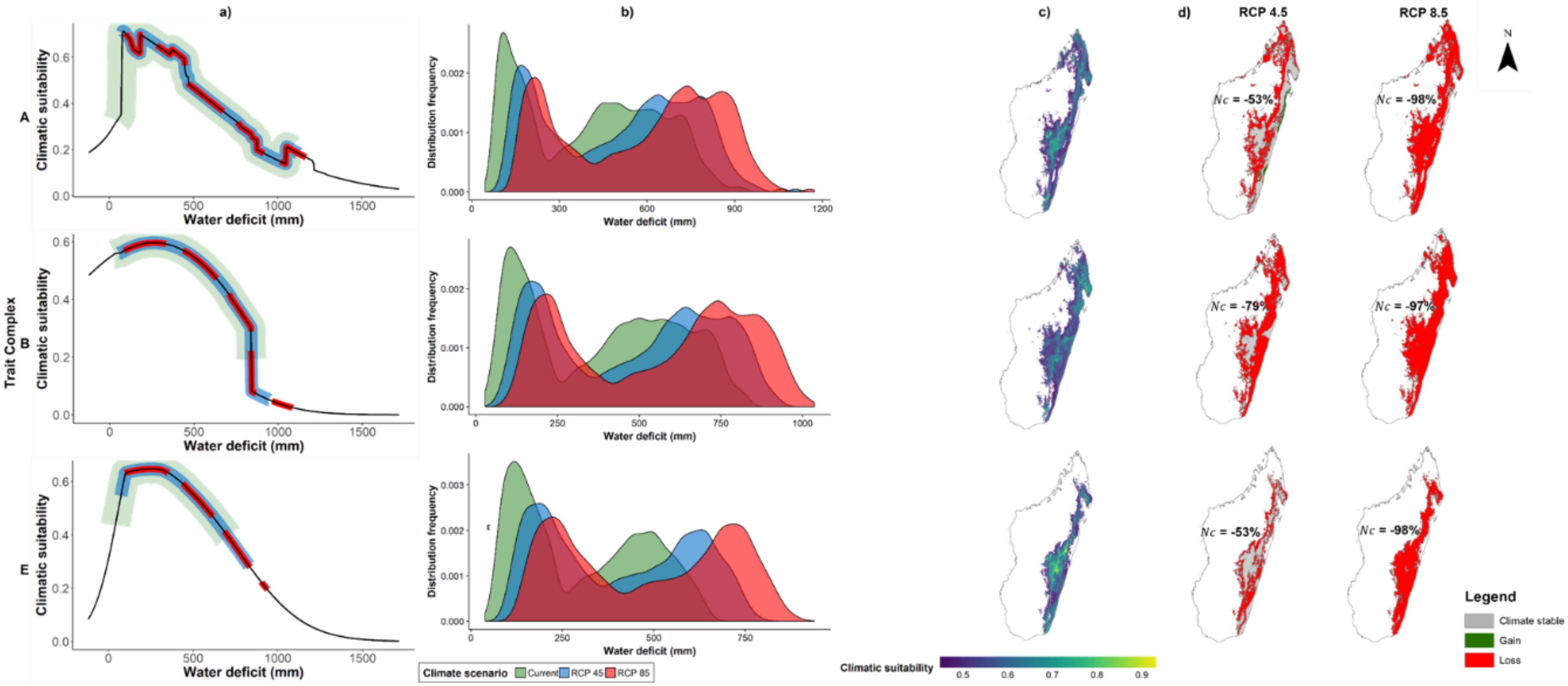
To validate our models, we created i) spatial overlap and ii) confusion matrices of raw data. To create a spatial overlap, we removed species from a complex and overlaid the removed species' range on the geographic range of the complex (modelled using the remaining species). A coarse expectation would be, if a complex can detect a component species well, that the area of spatial overlap should closely match the area of the species' range. Narrow ranging species are better accounted for than wide ranging species; through a generalised additive mixed model (GAMM) the smoothing term for the optimal GAMM on species range was significant ($F_{4,239}$= 299.3, $p < 0.001$). As species ranges decrease, TDMs better predict species presence through the spatial overlap. Overall, 83.6% of the variation in spatial overlap can be explained by the species range. However, the real validation of performance (accuracy) of TDMs is better measured through confusion matrices on raw species occurrences and spatial overlap, and TSS, to fully describe the sensitivity and specificity of the framework's ability to detect component species (Fig. 3) (Allouche et al., 2006). Accuracy of TDMs on predicting where in the landscape species are, was significant (t = -19.39, df = 213.14, $p < 0.001$; Fig. 3c). Both smoothing terms from the second GAMM were significant; model accuracy (TSS) improved when both the number of distribution records (Fig. 3d; $F_{5,188}$ = 4.113, $p = 0.001$) and range size (Fig. 3e; $F_{5,188}$ = 4.696, $p < 0.001$), decreased. Thus, TDMs can detect where in a landscape component species are likely to occur, even when such species have few spatial data.

Next page: *Fig. 3. Validation of TDMs.* ***a****) Illustration of methods; as an example, only an area of Northern Madagascar is shown. The extent of a trait complex distribution (dark green) is calculated without species x. The range of species x is overlaid (black outline) and the spatial overlap between range and complex is calculated (grey). To validate whether TDMs could predict where in the landscape species occur, raw occurrence data of individual species (black frog symbols) were overlaid on trait complex distribution (Calibration) and on spatial overlap (Test). The example shown in* ***a****) is for Test state. All other species were randomly sampled as true negatives (white frog symbols) and false positives (green frog symbols). True Skills Statistic (TSS) was then calculated from confusion matrices (****b****) for each state.* ***c****) TSS for Test significantly increased from Calibration (t = -19.39, df = 213.14, p < 0.001) and suggests that TDMs can predict where in the landscape species are likely to occur. Orange dots indicate the spread of data points. Plot whiskers extend to the smallest/largest value no further than 1.5 * interquartile range. Results from a GAMM show that TSS Test has a significant relationship with (****d****) the number of occurrences of a species (*$F_{5,188}$ *= 4.113, p = 0.001) and (****e****) the species range (*$F_{5,188}$ *= 4.696, p < 0.001). As both occurrences and range sizes decrease, the accuracy of TDMs improves. Smoothers are shown as blue lines and grey shaded areas are the 95% confidence interval.*


a)
Extent of species range
Spatial overlap
Extent of complex
N
0 5 10 20 Kilometers
Predicted
b)
Observed
Frog species 1
Any other frog species
Frog species 1
Any other frog species
True positive
False positive
False negative
True negative
TSS
c)
TSS
1.0
0.5
0.0
-0.5
Calibration
Test
Validation state
d)
TSS
0.8
0.4
0.0
0
50
100
Number of occurrences
e)
TSS
1.00
0.75
0.50
0.25
0
50000
100000
150000
200000
Species range (km 2)

We found that the spatial distributions of trait complexes (A, B and E) that contained threatened Malagasy amphibians exhibited strong correlations with climatic gradients, indicating high climate sensitivity, driven by an approximately gamma-shaped response to maximum water deficit (a measure of the length and severity of the dry season; Fig. 4a). Water deficit had a consistently high contribution to the models of threatened species complexes A, B and E (80%, 87% and 76% respectively) and for generalist complexes C and D (72% and 85% respectively) but was less important for generalist complex F (55%). Because of species composition in trait complexes, complexes occur over a wider range of climatic conditions than would be tolerated by a single species. Therefore, response curves may exhibit long slopes or minor peaks and troughs as each individual species contributes to the curve. Response curves of complexes A and E were similar both in intercept and shape. These two complexes share a general preference for forest floor/low vegetation (< 2 m) but differ in their habitat breadth and altitudinal range; complex E is composed of specialists. For both complexes the response curves suggest a need for a dry season and some tolerance of prolonged dry conditions: climatic suitability nears 0 at water deficit c. 1,500 mm yr^{-1}. Dry seasons are important for many species of Malagasy amphibians where a short dry season typically followed by heavy rains is a common breeding cue, particularly for those species which lay their eggs terrestrially (Glaw and Vences, 2007). These complexes (A and E) may be more tolerant to dry conditions as larvae are found in pools or streams and are less exposed to variation in water deficit. Adult habitat use suggests that they may experience a greater level of thermal buffering and environmental stability (De Frenne *et al.*, 2013) than arboreal heterospecifics. Complex B (arboreal species) demonstrated a narrower tolerance of dry conditions, with climatic suitability decreasing rapidly at water deficit c. 800 mm. The reduced tolerance of arboreal species to dry conditions is possibly linked to the avoidance of desiccation at various life history stages. Both eggs and larvae are typically deposited in arboreal water bodies (phytotelmata), which, due to the small size of the phytotelmata, are susceptible to drying out with adverse effects on eggs and larvae. We can conclude that regardless of complex that the length and severity of the dry season is a critical driver for amphibians, which reflects their intrinsic dependency on hydric and thermal interactions. Therefore, we expect that changes in climate which affect the dry season character are likely to have a notable impact on extinction risk.

Fig. 4. The response of threatened species trait complexes A, B and E to Water Deficit (WD), their spatial distribution under current climate and net changes in distribution for two end of century scenarios (RCP 4.5 and RCP 8.5). ***a****) Trait complexes are strongly correlated to climate, driven by WD (a measure of the length and severity of the dry season). The black lines show the variation of climatic suitability against WD. The range of WD for each complex is shown for current climate (thick green line), RCP 4.5 (blue line) and RCP 8.5 (long dashed red line). Across each complexes' range, WD shifts to the right, indicating a decreasing climatic suitability under seasonally drier conditions. Response curves suggest that arboreal species (complex B) are intolerant of dry conditions.* ***b****) WD changes across complex ranges, with curves shifting to the right as climate across ranges becomes seasonally drier. The spatial response of complexes is shown for current climate (****c****) and the impact of climate change driven by changes in WD on current distributions is given for future scenarios (****d****). The Index of net change (Nc) is given as a percentage change in range size.*

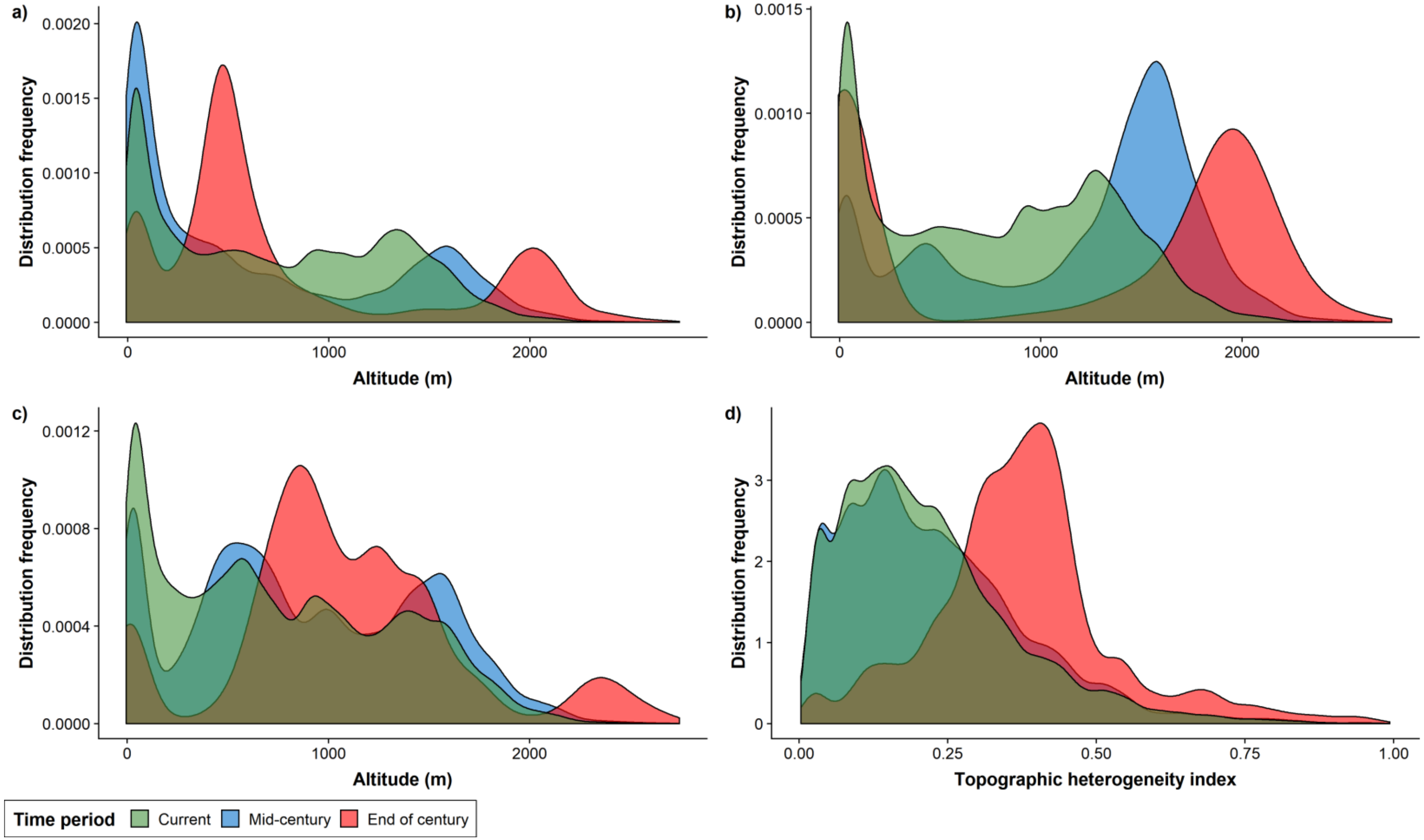


To assess climate change vulnerability of trait complexes, we considered two Representative Concentration Pathways (RCP4.5 and RCP8.5) of the Intergovernmental Panel on Climate Change's Fifth Assessment Report (IPCC-AR5; IPCC, 2013). We assessed the response of trait complexes to climate using an index of net change (Nc), to provide a percentage change in future range sizes when compared to current distributions, where negative values indicate range reduction and positive values indicate range increase. The impact of climate change on trait distribution is driven primarily by changes in water deficit; current ranges of complexes are set to become seasonally drier over time and saturated regions will decrease in area (Fig. 4b). By 2085 under RCP 4.5 (Fig. 4d), we projected a large range reduction in both complexes A (understorey species) and E (habitat specialists) (Nc; complex A = -53%, complex E = -53%), and the effect on complex B (arboreal species) was even greater (Nc = -79%). It is possibly the intimate relationship between complex B and vegetation which exacerbates its climate vulnerability, exposing obligate arboreal species to wider environmental variation and associated localised desiccation. Under RCP8.5 (Fig. 4d) there were severe reductions in ranges for complexes representative of threatened species (Nc, complex A = -94%, complex B = -97%, complex E = -98%). For more generalist complexes, the indicated losses were less but still of concern with c. 40-63% reduction for trait complexes characteristic of non-threatened species. Our models focussed explicitly on climate variables and did not include vegetation characteristics. As habitat may offer refugia, allowing species to mediate their response to climate through behavioural modification, notably arboreal species (Scheffers *et al.*, 2013), models based solely on macroclimate may be overly pessimistic. However, the observed range reductions are of concern and indicate a worrying future trajectory through range-associated species losses for threatened Malagasy amphibians.

Our results indicate that mid-century hold-outs (populations that are cut-off and temporally restricted in unusual microclimates; Hannah *et al.*, 2014) are likely to concentrate in the mid-altitudinal range (800 m – 1,400 m asl; Fig. 5), particularly for complexes B (arboreal species) and E (specialists). These areas, and connecting habitat pathways, should be priorities for conservation under climate change. Expected high elevation refugia were evident for end of the century distributions in all complexes, but complex E showed a distinct mid-altitudinal concentration and complex A was massed mainly around low-to-mid altitudes. The observed mid-altitudinal concentrations are caused by moisture balance and highlight the intricate dependency between amphibians and their environment, relying on the combination of moisture and thermal variables, rather than depending solely on thermal refugia (upslope shifts). Topographically derived refugia are likely to influence species' responses to climate shifts (Dobrowski, 2011), and although these are difficult to discern at the 1 km scale we used, this may be an underlying reason for the concentration of complex E species (Fig. 5) in topographically heterogeneous regions by the end of the century. The implications for conservation are that these mid-altitudinal ranges are critical for protection to help ensure species survival under climate change. Maintenance of connectivity pathways between altitudinal zones will help species disperse, however absolute distances for amphibian dispersal will be restricted (Smith and Green, 2005) and will further depend on their life history traits and extrinsic dispersal barriers.

Considering the level of climate change vulnerability our results suggest for Malagasy amphibians, we raise an urgent call for both assessments of their extinction risk and the conservation plans they inform, to consider the threats associated with climate change. This adds to a growing call for climate change vulnerability to be comprehensively included into IUCN Red List assessments (Foden *et al.*, 2013; Foden and Young, 2016; IUCN SSC Standards and Petitions Subcommittee, 2017). TDMs provide a pragmatic way to meet this need by facilitating assessment of the large number of taxa that were previously excluded from conservation planning and have much wider potential utility to assess future impacts on other rare, narrow-ranging or otherwise data-poor species. While data scarcity and small distribution ranges have previously posed assessment hurdles (Foden *et al.*, 2018), the TDM approach avoids many data requirement constraints (Keith *et al.*, 2008; Anderson *et al.*, 2009) yet still captures influential aspects of ecology and life history and produces the spatially-explicit outputs valuable for conservation planning. We show that TDMs perform well in regions with complex topographies, which also tend to be those that support high levels of species richness and genetic diversity due to historic speciation and environmental stability. Because such areas are vital as havens for species in the face of accelerated climate change (Keppel *et al.*, 2012), TDMs also assist in effective positioning of protected areas (Hannah *et al.*, 2007). Ultimately TDMs provide a valuable addition to the growing toolbox for conservation planning and management in the face of a rapidly changing climate.

*Fig. 5. Distribution frequency of climate suitability over altitude for trait complexes A (terrestrial adults), B (arboreal obligates) and E (habitat specialists). Distribution of climate suitability is considered for current climate, mid-century and end of century. Climate suitability shifts upslope for complexes A (**a**) and B (**b**), with mid–to-high altitudinal regions becoming increasingly vital mid-century for species survival. The mid-altitudinal range (800 m – 1,400 m asl) will be of greater importance for habitat specialists (complex E) as the century progresses (**c**). Complex E also shifts into areas of greater topographic heterogeneity (**d**) by the end of the century which may dampen extinction risk through the formation of microclimate refugia.*



2.3 Methods

Our TDM framework was developed to provide a pragmatic method of CCVA that provides spatial outputs even for those species lacking sufficient data for SDM. The first step was to obtain (qualitative) trait information for each species, by reviewing species accounts (Glaw and Vences, 2007; AmphibiaWeb, 2014; IUCN, 2014, 2017) and peer-reviewed literature. As Malagasy amphibian taxonomy is constantly evolving (Vieites *et al.*, 2009), we used the IUCN Red list (2014) as the reference point. We generated a list of 248 species of Malagasy amphibians (Appendix II) with search criteria at species level of Taxonomy 'anura', Location 'Madagascar' with location modifiers of 'native' and 'introduced'.

We applied Categorical Principal Components Analysis (CATPCA) (Vaughan and Ormerod, 2005; Linting and van der Kooij, 2012) to the trait data, to produce a latent variable capable of describing the relationship between several traits. We ran an initial CATPCA on species' traits, stipulating six dimensions (analogous to the number of variable categories). Missing trait values for each species were treated as an additional category to obtain an optimal nominal quantification, based on the marginal frequencies of the category, and determine whether individual species were unique or belonged to similar groups (Linting and van der Kooij, 2012). We retained all variables (traits) within each model as all variables contributed to the principal components i.e. variables whose centroid coordinate means were > 0.1. In each model iteration we removed dimensions where eigenvalues were < 1 and accounted for < 30% of the variance (Linting and van der Kooij, 2012). A final CATPCA was run on six variables retaining two dimensions. Cronbach's alpha reliability coefficient was used to confirm dimension consistency. CATPCA was carried out using IBM SPSS 24 for windows.

2.3.1 Identifying trait complexes and environmental response

The dimension object scores produced from the final CATPCA determined species membership of a cluster by K-means cluster analysis. An assumption of cluster analysis is that there is no collinearity between variables; ordination before clustering removes collinearity between variables. We ran 10,000 iterations of K-means cluster analysis and determined the optimum number of clusters from the elbow of the total within sum of squares across the clusters. Final cluster centres were used to define the cluster as ecological groups (complexes) and we then linked and pooled distribution records (GBIF.org, 2013; HerpNET, 2014) for component species of a complex. In total there were 2990 distribution records with most observations from Least Concern species (76%, 2278 records, 109 species). Threat categories together accounted for 10% of records (Vulnerable: 6%, 165 records, 31 species; Endangered: 4%, 127 records, 28 species; Critically endangered: 1%, 27 records, 8 species). Near Threatened and Data Deficient species accounted for the remaining 13% (393 records) of occurrences. Distribution records were spread across complexes as follows: complex A, 861; complex B, 394; complex C, 386; complex D, 247; complex E, 344 and complex F, 758. Prior to pooling, distribution records were cleaned to remove inconsistencies. Firstly, we removed incorrect taxa or species not fully identified. We then removed records with no author identification, missing coordinates (latitude and longitude) or imprecise geo-references/locality information. Remaining data were then visually inspected in ARCGIS for each species and any occurrences assigned outside the extent of Madagascar were removed. Cluster analysis was performed using the Cluster package (Maechler *et al.*, 2018) for R for Windows (version 3.2.4) (R Core Team, 2018).

Relationships of complexes with climate were assessed along four climatic gradients (Table 3), using MaxEnt (v. 3.3.3k) (Phillips *et al*., 2006) to estimate an index of relative suitability (Phillips *et al*., 2006; Pearson, 2010; Anderson and Gonzalez, 2011). Climatic variables were selected based on biological relevance to amphibians and low intercorrelation (Pearson's $r < 0.7$). Baseline conditions (1950-2000) were derived from WorldClim (Hijmans *et al.*, 2005) at 30 arc-sec (c. 1 km) resolution; for area calculations we used the Africa Albers Equal-area projection at 900 m resolution. We set MaxEnt to logistic output, 500 iterations and used all feature classes as suggested by the default settings. We corrected for geographical sampling bias by using a kernel density bias file (Fourcade *et al.*, 2014) derived from all amphibian observations and we sampled one occurrence per grid cell at 1 km (Fourcade *et al.*, 2014). MaxEnt limits model complexity and overfitting through regularization (β) (Phillips *et al*., 2006; Radosavljevic and Anderson, 2014). To determine the best value for β, we compared individual models for each complex using Akaike Information Criteria (AIC_c) (Warren *et al*., 2010; Warren and Seifert, 2011), where β was set from 1 to 10. Finally, we jack-knifed environmental data to determine variable importance in model performance. Model performance was validated using the mean Area Under the Curve (AUC) statistics from threshold independent Receiver Operating Characteristic (ROC) plots of ten models. We also used True Skills Statistic to assess model performance, due to its independence from prevalence and ability to reflect sensitivity and specificity (Allouche *et al*., 2006). Threshold values for trait distributions (0.5 prevalence) were derived from Maximum test sensitivity plus specificity logistic threshold (Liu *et al.*, 2005; Bean *et al*., 2012; Liu *et al*., 2013).

To assess climate change vulnerability of trait complexes, we considered two Representative Concentration Pathways (RCP4.5 and RCP8.5) of the Intergovernmental Panel on Climate Change's Fifth Assessment Report (IPCC-AR5; IPCC, 2013) projecting global temperature anomalies of 2.4°C and 4.9°C by 2085 (at atmospheric CO_2 equivalents of 650 and 1370 ppm) respectively. Pathways were chosen because they represented an intermediate mitigation or stabilisation scenario (RCP4.5) and a high emission scenario (RCP8.5) (van Vuuren *et al*., 2011). We evaluated the response of trait complexes to climate using an index of net change (Nc; equation 1).

Equation (1).

$$Nci = \sum_{i} \frac{\left(T_{fi} - T_{fd}\right)}{T_c}$$

The index of net change in area (Nc) for each future scenario is calculated for each trait complex (i), as the sum of the change for a future scenario; future increase in area (T_{fi}) (km^2) minus future decrease in area (T_{fd}) over the trait area under current climate conditions (T_c).

2.3.2 Validation of TDM

Overall TDM accuracy was assessed by AUC and TSS. For AUC we used a cut-off of > 0.7 to discriminate between poor and good models (see Landis and Koch, 1977). In order to determine a 'good' model score for TSS, we used values suggested by kappa, a similar approach, where scores > 0.4 are considered good (Landis and Koch, 1977), whilst models with scores of 0 to -1 perform worse than random (Allouche *et al*. 2006).

Trait complexes were validated by: i) a Generalised Additive Mixed Model (GAMM) and ii) confusion matrices assessed by TSS. Prior to validation, we calculated the spatial overlap between a complex and range of component species *x*. Within each trait complex, we iteratively removed member species and then modelled the remaining composite species of a complex. The spatial distribution of removed species was then overlapped on the spatial distribution of their complex (i.e. spatial overlap). Species distributions for each removed species were either obtained from SDM binary presence/absence maps or IUCN range maps (IUCN, 2014) (Minimum Convex Polygons; MCPs). Modelled species distributions were preferred over range maps based upon MCPs as MCPs may over or underestimate the true area of occupancy (Burgman and Fox, 2003; Jenkins *et al.*, 2014). However, for species that could not be modelled (i.e. n < 10), IUCN MCPs were the most pragmatic and accurate option. The relationship between spatial overlap and variables not included in the trait complex model, was initially tested by a Generalised Linear Mixed Model (GLMM). This allowed us to see how well the complex accounted for its component species. Variables external to the trait complex model were collinear and only species range and IUCN threat status were retained as fixed factors and trait complex was included as a random effect to allow fixed effects to vary for each trait complex. However, through the residuals we suspected an underlying pattern and fitted a Loess smoother term to species range within a GAMM (Zuur *et al.*, 2009).

To further investigate how species were related to their complex, we overlaid raw occurrence data for each species on i) their complex range (calibration) minus that species and ii) on their spatial overlap (test). We then randomly sampled all other species occurrences as true negatives and false positives (Ferrier and Guisan, 2006) to create a confusion matrix (Fielding and Bell, 1997) and report TSS. A confusion matrix allows more comprehensive analysis than mere proportion of correct classifications (accuracy). TSS avoids prevalence and gives more information about the balance between sensitivity (true positive rate) and specificity (true negative rate) (Allouche *et al*., 2006). In doing so, TSS provides detail on whether TDMs can correctly predict species locality in the landscape. If species' ranges are being effectively discriminated by TDMs, then the TSS should reflect both a good true positive rate and true negative rate by being above 0.4 (good model) and preferably close to 1 (perfect detection). Changes in TSS between calibration and test were assessed by a Welch two sample t-test in R. To understand which variables influenced TSS on spatial overlap, we ran a second GLMM. TSS was the dependent variable, and species range, number of occurrences (1 km resolution), proportion of spatial overlap were fixed factors and trait complex was the random effect. Again, due to underlying patterns in the residuals, we fitted a smoothing curve to both species range and number of occurrences within a GAMM. The GLMM and GAMM were analysed with R for Windows (version 3.2.4; R Core Team, 2018) with packages Lme4 (Bates *et al.*, 2015) and mgcv (Wood, 2004, 2017) respectively. For all statistical tests $\alpha = 0.05$, two tailed.

2.4 References

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2.5 Supplementary

Table S1. Ecological grouping (functional trait complexes) of Malagasy amphibian species.

Complex	Number of species per complex	Trait complex interpretation
A	80	Understorey species (fossorial/terrestrial or low vegetation), typically restricted two habitat types ($\bar{x}$ = 2.29, SD ± 0.363) with a mean altitudinal range of 675 m (SD ±30 m). Preference for aquatic (streams or pools) or terrestrial sites for egg deposition. Aquatic larvae (ponds or streams).
B	27	Arboreal species with a reliance on phytotelmata for egg and larval deposition.
C	10	Medium bodied generalists. Medium sized frogs ($\bar{x}$ = 50.267 mm, SD ±11.365 mm), broad habitat width ($\bar{x}$ = 4.5, SD ±1.958), large altitudinal range ($\bar{x}$ = 1830 m, SD ±512 m) and species range ($\bar{x}$ = 99546 km^2, SD ±60373 km^2). Larvae are always aquatic.
D	17	Semi-arboreal to arboreal with eggs typically deposited overhanging water. Medium altitudinal range ($\bar{x}$ = 675 m, SD ±364 m).
E	59	Narrow altitude range habitat specialists. Semi-aquatic/Terrestrial and semi-arboreal adults, egg deposition predominately either in streams or terrestrial. Habitat restricted species/specialists (one habitat type) with narrow altitudinal range ($\bar{x}$ = 223 m, SD ±208 m) beginning at $\bar{x}$ = 734m asl. Small body size ($\bar{x}$ = 27.880 mm, SD ±8.525 mm).
F	47	Habitat generalists with restricted altitudinal range. Occupying several habitat types ($\bar{x}$ = 3.688, SD ±1.518) and a more restricted altitudinal range than complex C ($\bar{x}$ = 955 m, SD ±292 m). Body size $\bar{x}$ = 43.033 mm, SD ±22.885 mm.

Table S2. Climatic gradients used in analysis.

Climate variable	**Description**
Maximum water deficit (mm)	Consecutive months that experience rainfall < monthly PET (Potential Evapotranspiration, Hargreaves method), over which the shortfall in rain is accumulated.
Temperature seasonality (^{0}C x 10)	Standard deviation over monthly values
Rainfall wettest quarter (mm)	Any consecutive three-month period
Mean temperature of the warmest quarter (^{0}C x 10).	Any consecutive three-month period

Chapter 3. Interactions between amphibian traits, climate and habitat under predicted climate change

Preface

Trait distribution models (TDMs, Chapter 2) highlighted concerning range contractions for trait complexes of Malagasy amphibians. These contractions suggest an alarming loss of amphibian species by 2085, particularly among species that demonstrate obligate arboreal traits. However, these models demonstrate a broad climate envelope and whilst we know that broad scale amphibian distributions are highly correlated with temperature and precipitation gradients (Buckley and Jetz, 2007), at finer spatial scales, amphibian presence in the landscape depends on the availability of suitable habitat (Opdam and Wascher, 2004; Cushman, 2006; Almeida-Gomes *et al.*, 2016). Therefore, it is useful to investigate whether adding habitat variables to TDMs can improve model performance and therefore better inform conservation management of amphibian habitat.

This chapter is written in the style of *Biological Conservation.*

3.1 Abstract

Trait Distribution Models (TDM) have shown that predicted climate change threatens amphibian species in Madagascar. However, assessing amphibian distribution dynamics solely on climate variables may not contain enough information for conservation action. Here we investigate whether inclusion of habitat variables improved TDM models beyond models comprised solely of climate variables for predicting the impact of climate change on Malagasy amphibians. we used a null model construct to build three model variants; climate only, habitat only and climate and habitat and compare model performance using Area Under the Curve (AUC) and True Skills Statistic (TSS), as well as sensitivity and specificity. Climate-only models were also assessed for over-prediction compared to other model variants, and we tested whether overprediction was related to the level of species specialisation as measured by niche breadth. Finally, key drivers responsible for the distribution of Malagasy amphibians were determined from the best performing model type. The inclusion of both climate and habitat variables significantly improved TDM specificity and model performance, particularly for trait complexes that reflect specialised habitat requirements: climate-only models over-predicted spatial distributions by up to 60% for specialised species but not for generalists. Amphibian trait distributions are correlated with the structure of vegetation and the length and severity of the dry season, but the precise response to climate and habitat varied with trait complex. Given the heavy anthropogenic demands on ecosystems in Madagascar, habitat restoration and non-use protections may not always be a financially viable and sustainable option. In these cases, management that retains specific trees for their height and structural attributes and allows some human access and use may be a more realistic goal. The inclusion of both climate and habitat variables in the model structure is essential for specialist species and on that basis, TDMs can indicate spatial priorities for conservation management under predicted climate change. We propose that assessment of functional traits should underpin habitat management strategies in conjunction with adaptive habitat management strategies.

Keywords: Amphibians, Madagascar, habitat specialists, vegetation structure, climate over-prediction, community management.

3.2 Introduction

Amphibians are a highly threatened taxonomic group which are often seen as bioindicators of wider habitat health due to high dependency on their immediate environment (Nori *et al.*, 2015). Because of their environmental dependency, amphibians are considered vulnerable to climate change, with individual species vulnerability dependent on a combination of their functional traits, adaptive capacity and ability to disperse. Trait Distribution Models (TDM) indicate that predicted climate change threatens anuran (frog) species in Madagascar, with some functional groups, such as arboreal specialists, being more vulnerable than others (Chapter 2). However, we know that habitat characteristics are important determinants of amphibian distributions (Cushman, 2006; Almeida-Gomes *et al.*, 2016). Therefore, assessing amphibian distribution dynamics solely on climate variables may not contain enough information for conservation action, particularly for identifying habitat management strategies; we could be in danger of over-simplifying the challenge, resulting in misdirected recommendations. Understanding how species are distributed with respect to habitat character, what the key landscape drivers of distribution are, will ultimately be beneficial for managing landscapes for conservation of threatened species under the combined impacts of climate change and habitat loss (Peters and Darling, 1985; Ackerly, 2003; Heller and Zavaleta, 2009; Keeley *et al.*, 2018).

As demonstrated in Chapter 2, TDMs populated with climate data provide a broad climate envelope for the distribution of amphibian trait complexes. However, niche modelling, which includes both TDMs and Species Distribution Models (SDMs), has struggled to bring together multi-scale drivers (Fournier *et al.*, 2017) and despite the documented importance, there is a lack of integration of climate and habitat into modelling (Sirami *et al.*, 2017). It has been broadly assumed that climate overrides habitat at the larger regional scales (Thuiller *et al.*, 2004), whilst habitat is more important at the local level (Bailey *et al.*, 2002). Therefore, climate-only studies and habitat-only studies are commonplace (Sirami *et al.*, 2017), and these singular objectives may prove detrimental to conservation by failing to account for combined effects. Using the broad climate envelope for conservation decisions is something akin to relying on extent of occurrence for local scale habitat management. For example, to mitigate the impacts of climate change, climate pathways to and from mid-altitudinal areas have been identified as priorities for conservation (Heller and Zavaleta, 2009; Mawdsley *et al.*, 2009; Hodgson *et al.*, 2011; Beier, 2012; Gregory *et al.*, 2014; Hannah *et al.*, 2014). Yet, underlying those climate pathways is uncertainty about the distribution and quality of habitats in the landscape, on which connective pathways will depend (Hodgson *et al.*, 2009). In a way, the segregation of studies into climate-only and habitat-only is surprising; ecological systems are scale dependent and hierarchical in nature (Cushman and McGarigal, 2002). Simplified, the environment acts as a filter at different scales removing species without the necessary traits for survival (Keddy, 1992; Fournier *et al.*, 2017). Filters work at different levels; climate governs broad-scale processes and in turn dictates habitat. Habitat then influences microclimate and local climate, therefore interactions between climate and habitat should be considered normal, not an exception (Parmesan *et al.*, 2013; Sirami *et al.*, 2017). TDMs are community-based models which use species' traits to assess the distribution of communities along environmental gradients and are subject to the assembly rules proposed by Keddy (1992). As such, the effects of environmental filtration should be apparent, particularly in a taxon with a strong reliance on climate and high philopatry to the landscape, such as amphibians. Broad scale amphibian distributions are highly correlated with temperature and precipitation gradients (Buckley and Jetz, 2007), but at finer spatial scales, amphibian presence in the landscape depends on the availability of suitable habitat (Opdam and Wascher, 2004; Cushman, 2006; Almeida-Gomes *et al.*, 2016). Furthermore, functional traits are closely linked to species response to the landscape character (Duflot *et al.*, 2014) and therefore will respond more to habitat transformation (Pineda and Halffter, 2004) than a change in climatic conditions. Without understanding how amphibian traits respond to habitat, we reduce our effectiveness in deciding the most appropriate management strategies for conservation.

TDMs for Malagasy amphibians, which account for the impact of habitat as well as environment, would be a valuable conservation tool. More than 90% of Madagascar's natural forest has been lost and what remains is highly fragmented (Ganzhorn *et al.*, 2001; Hannah *et al.*, 2008), a situation that is becoming increasingly worse (Harper *et al.*, 2007; Ramiadantsoa *et al.*, 2015). A proposed strategy for allowing species dispersal and attenuating the impact of climate change for Madagascar is to restore habitat between fragments, notably riverine corridors, reducing the extinction risk due to climate change (Hannah *et al.*, 2008; Hodgson *et al.*, 2011; Brown *et al.*, 2015). Whilst habitat restoration is a common-sense approach to climate mitigation (Heller and Zavaleta, 2009), such corridors may not be achievable with respect to cost and community dependency on local forests (Hannah, 2010). Much of the management of natural resources in Madagascar has devolved to local communities (Fritz-Vietta *et al.*, 2009; Rasolofoson *et al.*, 2015; Gardner *et al.*, 2018) and there is heavy reliance on remaining forests to meet the needs of the country's growing population (Borgerson *et al.*, 2018). However, questions exist around whether habitat management strategies and vegetative character will be suitable for many species, particularly habitat specialists (Rosa *et al.*, 2012).

To provide an indication of management action for threatened species groups through TDMs, I used a null model to compare models of climate variables only, habitat variables only and climate and habitat variables together, allowing an assessment of the attributable impacts of each model variant (habitat or climate) as well as the cumulative impacts (climate and habitat) on Malagasy amphibians. We hypothesise that combined climate and habitat models will demonstrate improved performance compared to other model variants. Furthermore, climate-only models will also overpredict distributions of trait complexes, as functional traits of amphibians are closely tied to the landscape, broad distributions of traits are constrained by climate and traits are subject to hierarchical environmental filtering. On the same basis, the more specialised the species/complex (niche breadth), the greater the overprediction should be. We then apply TDMs to ask what the key drivers of distribution are for Malagasy amphibians and consider the implications for habitat management.

3.3 Methods

In Chapter 2, we used the TDM framework to produce distributions of trait complexes of Malagasy amphibians. Detailed species accounts for many newly described species in Madagascar are sparse, therefore, species trait data were derived from the IUCN Red List (2014) as a baseline for amphibian species in Madagascar (total of 248 species). Within the TDM framework, trait data are collected for each species and subjected to Categorical Principal Component Analysis (CATPCA) performed with SPSS 24.0 (IBM Corp, 2016). Species are then grouped by K-means clustering into complexes, occurrences combined and then complexes are mapped by a Species Distribution Model (Chapter 2). K-means clustering was carried out using cluster package (Maechler *et al.*, 2018), available with the R software (version 3.5.0; R Core Team, 2018). Six trait complexes (A to F) were identified in Chapter 2; complexes A, B and E represent most threatened species (IUCN Vulnerable to Critically Endangered; IUCN, 2014) in Madagascar (88%), where A = understorey species with restricted habitat (hereon referred to as "understorey species"), B = arboreal species and E = specialists with narrow altitudinal range (hereon referred to as "specialists"). Complexes C, D and F represent habitat generalists, with C representing large bodied, generalists with large range sizes. Because of their conservation importance, throughout this chapter we focus on the three threatened species complexes – A, B and E.

All trait complex distributions were modelled using MaxEnt (v.3.3.3k; Phillips *et al*., 2006) and cross-validated ten times. Each modelled distribution was debiased using a kernel density bias file (Fourcade *et al.*, 2014) derived from all amphibian observations in the dataset. We also determined the best value for regularization (control of model complexity and overfitting; β) by Akaike Information Criteria (AIC_c) available in ENM Tools (Warren, Glor and Turelli, 2010; Warren and Seifert, 2011). Finally, we created grids with cell sizes of 250 m resolution and sampled one occurrence per grid cell (Fourcade *et al.*, 2014). For range size calculations and all spatial datasets, we used the Africa Albers Equal-area projection.

3.3.1 Climate and habitat variables.

We used four climate and four habitat variables in analysis, (Table 1). Climate conditions (1950-2000) were derived from WorldClim (Hijmans *et al.*, 2005) at a 30 arc-sec (c. 1 km) resolution and were clipped to Madagascar for analysis. Water deficit (WD, mm) was developed from Potential Evapotranspiration (PET, Hargreaves method) and is defined as consecutive months that experience rainfall less than the monthly PET, over which the shortfall in rain is accumulated (Platts *et al*., 2010). Habitat variables were chosen as those known to be relevant to amphibians: topographic wetness, topographic heterogeneity, Enhanced Vegetation Index (EVI) and canopy height. Topographic wetness was derived from a 30 m filled Aster DEM (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2001). Topographic wetness is a measure of both the potential for water to flow into the cell, and how likely/long it is to stay there (steeper slopes have lower values). The filled 30 m DEM was used to create two rasters using ArcGIS 10.3.1 (ESRI, 2015); accumulation of water flow (w) from the combined upslope contributing area for each pixel and slope (s). Topographic wetness was then calculated from Ln(900w/tan(s)) and values were normalised. Topographic heterogeneity evaluates the ruggedness of the landscape, where high values reflect a varied landscape, using the elevational range in 300 m by 300 m neighbourhood. We also calculated mean annual Enhanced Vegetation Index from 16-day 250 m MODIS MOD13Q1 data (Didan, 2015) from the years 2007 - 2017. We preferred EVI to Normalised Difference Vegetation Index, as EVI better reflects variation in canopy structure and architecture (Vieilledent *et al.*, 2016). Both the ASTER DEM and MOD13Q1 Products were retrieved from the online Data Pool, courtesy of the NASA Land Processes Distributed Active Archive Center (LP DAAC, 2017). Canopy height was sourced from NASA Earthdata at 1 km resolution (Simard *et al.*, 2011; ORNL DAAC, 2017).

3.3.2 Evaluating inclusion of habitat variables in TDMs.

To identify the extent to which habitat variables improved TDM model performance, we compared the climate distribution to the habitat distribution of complexes through a null model. A null model allows us to identify important ecological process by holding certain elements of data static and allowing others to vary (Gotelli and McGill, 2006). Using MaxEnt, we built three test models:

climate-only, habitat-only and habitat+climate. A fourth model, with all predictor data randomised, functioned as a null hypothesis; that no pattern would be observed between locality data for amphibians and randomised environmental data. We used eight variables in each model (Table 1), which were selected because of their relevance to amphibians and moderate-to-low intercorrelation (Spearman's rho < 0.7; Dormann *et al.*, 2013) with the exception of canopy height and Enhanced Vegetation Index (Spearman's rho = 0.79). However, MaxEnt is considered robust to collinear variables (Phillips *et al*., 2006; Braunisch *et al*., 2013; Feng *et al*., 2019) and excluding such correlated variables has little impact on the model (Feng *et al*., 2019). Furthermore, we felt that both variables carried information relevant to amphibians. Therefore, we retained canopy height and Enhanced Vegetation Index as predictors. For the climate-only and habitat-only models we replaced habitat and climate variables respectively with randomised grids of original data, such that the spatial structure was removed but the mean and variance reflected the original data. Resolution for variables and randomised grids were set to 250 m. Where resolutions of original data differed (i.e. climate data) then datasets were resampled to 250 m resolution after processing, using bilinear interpolation (weighted distance average) in ArcGIS 10.3.1 (ESRI, 2015). We compared model specificity as the mean across ten models. We also report the True Skills Statistic (TSS) (Allouche *et al.,* 2006), Area Under the Curve (AUC) and model sensitivity. Model metrics were computed using the following packages in the R software (R core team, 2018): ROCR (Sing *et al.*, 2005), boot (Canty and Ripley, 2017) and vcd (Meyer *et al.*, 2017). For all statistical tests α = 0.05, two sided.

Table 1. Climate and landscape variables used in analysis.

Variable type	Variable code	Description
Habitat	TWI	Topographic wetness index
	EVI	Enhanced vegetation index. Higher values refer to abundant vegetation
	THI	Topographic heterogeneity/terrain ruggedness index. High values are a measure of variable landscape
	CH	Canopy height (m).
Climate	WD	Maximum water deficit (mm). Consecutive months that experience rainfall < monthly PET (Potential Evapotranspiration, Hargreaves method), over which the shortfall in rain is accumulated.
	TS	Temperature seasonality (^{0}C x 10). Standard deviation over monthly values
	RWQ	Rainfall wettest quarter (mm). Any consecutive three-month period
	TWQ	Mean temperature of the warmest quarter (^{0}C x 10). Any consecutive three-month period

Suitability maps were then used to obtain the percentage overprediction between climate-only models and the best performing model type identified above. From here, the relationship between species specialisation (niche breadth) and overprediction was assessed. We used ENMTools 1.4.4 (Warren *et al.*, 2010; Warren and Seifert, 2011) to calculate trait complex niche breadth from suitability maps derived from climate-only models and the best performing model type identified previously, across ten models. Changes in niche breadth between model types were assessed through non-parametric Friedman tests, followed by Nemenyi post hoc tests (Pohlert, 2014) on significant results. To determine whether increasing specialisation led to greater over-prediction, we used a generalised additive model (GAM) where the percentage of over-prediction for climate-only models was the dependent variable with a smoothing term fitted to niche breadth. Adjusted R^2 was used to account for the variance in data. The GAM was carried out using the mgcv package (Wood, 2011) in R.

3.3.3 Drivers of trait distribution

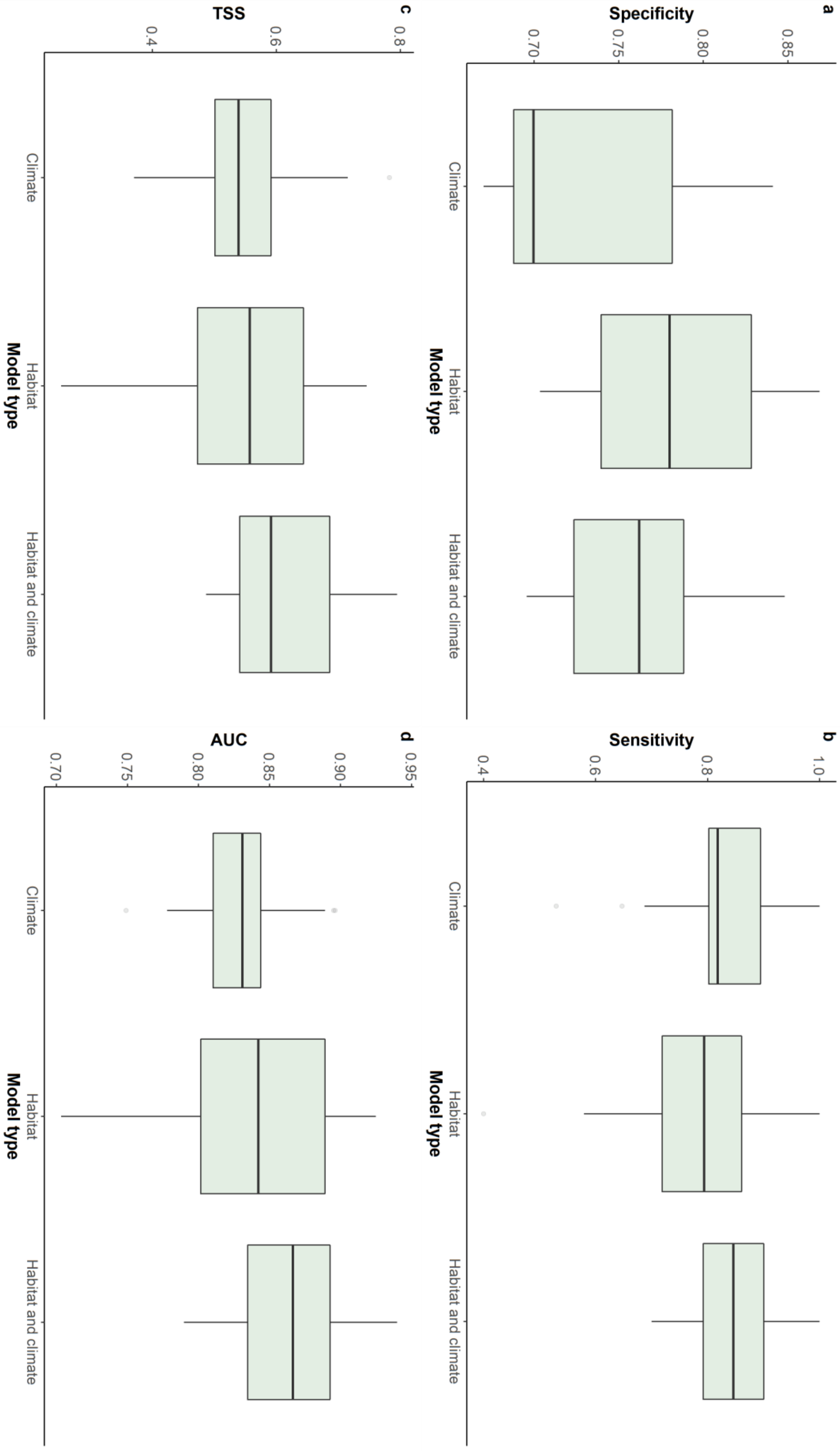
We used the best performing TDM in terms of model performance, determined by both TSS and AUC, from the comparison of climate-only, habitat-only and habitat+climate models and then determined drivers of trait distribution for understorey species, arboreal species and specialists (complexes A, B and E respectively). We jack-knifed environmental variables in MaxEnt to determine variable importance and from here we identified variables which contributed the most to the model and produced respective response curves to explain the observed distribution of the complex.

3.4 Results

3.4.1 Evaluating inclusion of habitat variables in TDMs

The null hypothesis model was no better than a random classifier, reflected by AUC values ($\bar{x}$ = 0.514); no patterns were observed between amphibian locality data and randomised environmental data, validating the decision to use randomised predictors in test models. All test models performed well, all AUC values were > 0.8 and all TSS values were > 0.5. Inclusion of habitat variables improved TDM complex specificity when compared to climate-only models (Fig.1; F = 7.728, df = 2, *p* < 0.001; between climate-only and habitat+climate, t = -2.3786, df = 51.594, *p* = 0.021; climate-only and habitat-only, t = 3.5967, df = 56.694, *p* < 0.001), but habitat-only models were the most specific. Model sensitivity did not change between model types, however models which contained both climate and habitat variables (habitat+climate) showed a significant improvement in overall performance in terms of TSS (Fig. 1c; t = -2.4997, df = 57.872, *p* = 0.015) and AUC (Fig. 1d; t = -4.0923, df = 56.973, *p* < 0.001).

Next page: *Fig. 1. Habitat variables improve Trait Distribution Model (TDM) specificity.* ***a)*** *Inclusion of habitat variables in TDMs improve the specificity over climate-only models (F = 7.728, df = 2, p < 0.001). Sensitivity (****b****) does not significantly change when habitat variables are included. However, inclusion of both climate and habitat variables significantly improves TDM performance for both (****c****) True Skills Statistic (TSS; t = -2.4997, df = 57.872, p = 0.015) and (****d****) Area Under the Curve (AUC; t = -4.0923, df = 56.973, p < 0.001). For all plots, the whiskers extend to the smallest/largest value no further than 1.5 * interquartile range.*


a
Specificity
0.70
0.75
0.80
0.85
b
Sensitivity
0.4
0.6
0.8
1.0
c
TSS
0.4
0.6
0.8
d
AUC
0.70
0.75
0.80
0.85
0.90
0.95
Climate
Habitat
Habitat and climate
Model type

Niche breadth differed between climate-only, habitat-only and habitat+climate models (χ^2 = 109.2, df = 2, $p < 0.001$). Models which contained both habitat and climate variables demonstrated a narrower niche breadth than climate-only models regardless of complex (W = 2330, $p = 0.005$). Conversely, the niche breadth for habitat-only models increased when compared to climate-only models. Climate-only models over-predicted for each complex, however, the amount of over-prediction varied depending on the complex (Fig. 2). Complexes with specialised traits have narrower ranges, and these in turn are more sensitive to over-prediction in climate-only models; the more specialised the trait complex, the greater amount of spatial over-prediction. The relationship between specialisation and over-prediction was determined by a GAM, where the smoothing term on niche breadth was significant ($F_{3, 29} = 22.28$, $p > 0.001$) and adjusted R^2 explained 68.8% of the variance. For specialist complexes where niche breadth is low (between 0.3 to 0.5), climate-only models over-predicted the area of suitable habitat by up to 60% compared to habitat+climate models (Fig. 3). As a further check, comparison was made with non-threatened trait complexes, and such over-prediction decreased for complexes composed of generalists with a very wide niche breath (niche breath, $\bar{x}$ = 0.881, over-prediction, $\bar{x}$ = 0.1%).

Inclusion of both climate and habitat variables significantly improved TDM specificity and model performance, particularly for trait complexes that reflect specialised habitat requirements. Climate-only models over-predicted spatial distributions by up to 60% for specialised species but not for generalists.

Fig. 2. The relationship between percentage area over-predicted by climate-only models and trait complex specialisation. Climate-only models show very little over-prediction for complexes with a more generalist niche breadth (the right of the x-axis). For specialised complexes on the left of the x-axis, such as complex B (arboreal specialists) and complex E (narrow altitudinal range and habitat type), then climate-only over-prediction rises to > 60%. As specialism decreases (right of the x-axis), then over-prediction decreases to < 20%, as demonstrated by complex A (understorey species). The smoothing term is significant (red line; $F_{3, 29}$ = 22.58, p > 0.001) and explains 68.8% of the variance in over-prediction. The shaded area represents a 95% confidence interval. The observed over-prediction suggests that for specialist species, both habitat and climate variables are needed to explain distributions.

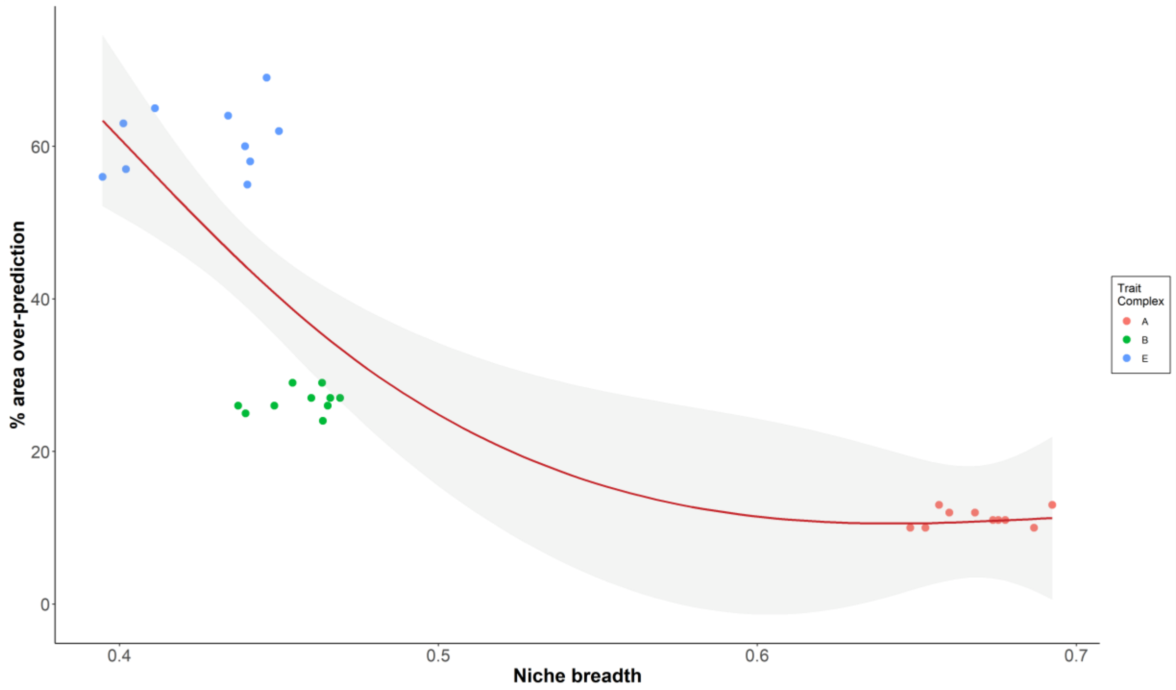
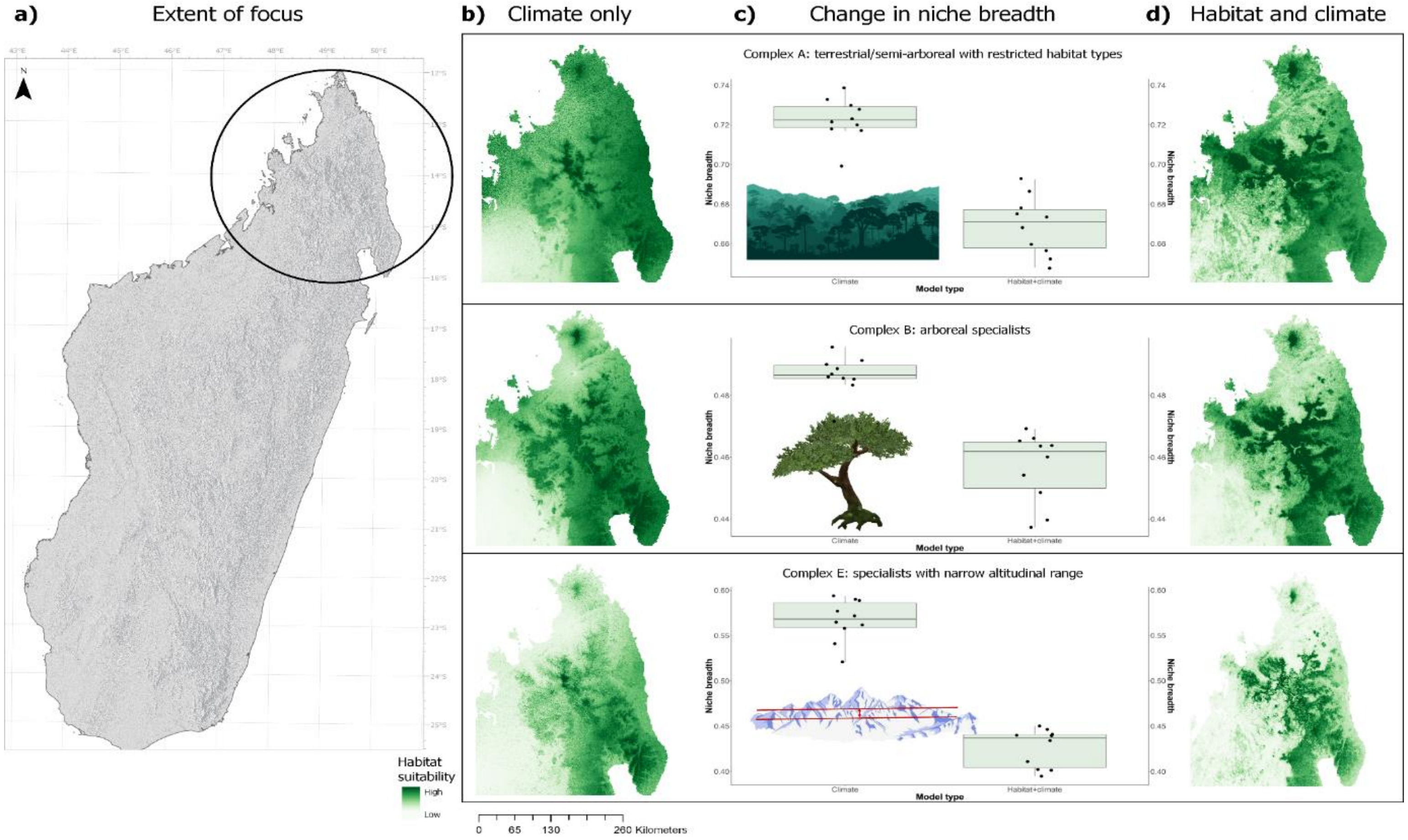


*Fig. 3. The change in niche breadth and habitat suitability between climate-only and habitat+climate models. To illuminate detailed changes between model types the extent of focus covers northern Madagascar (**a**) and is illustrated by the threatened species complexes A (understorey), B (arboreal) and E (specialists). Climate only models (**b**) over-predict habitat suitability when compared to habitat+climate models (**d**). **c**) Box plots demonstrate the change in niche breadth between climate only and habitat+climate models. In all cases, resource use is more restricted in habitat+climate models and has implications for conservation decisions.*



3.4.2 Drivers of trait distribution.

Amphibian trait distributions are correlated with the structure of vegetation and the length and severity of the dry season, but the precise response to climate and habitat varied with trait complex. Key drivers of Malagasy amphibian distributions were canopy height, EVI and water deficit (Table 2). For example, the contributions of these three variables in the MaxEnt model for understorey species (complex A) were 23%, 27% and 19% respectively, which suggested that vegetation characteristics and the length of the dry season are approximately equal in importance in explaining the distribution of the trait complex. Habitat suitability for understorey species and canopy height/EVI showed an initial linear relationship, after which suitability decreased or plateaued (Fig. 4a and b; maximum canopy height = 32 m, EVI = 0.42). The raised intercept of habitat suitability (0.1) for understorey species' EVI response curve, coupled with the peak at EVI = 0.42, indicated a tolerance of habitat types from shrubland to temperate/seasonal forest. The response curve of understorey species to water deficit demonstrated a low intercept for habitat suitability (Fig. 4c) and indicated that the complex cannot tolerate year-round moisture and requires a short dry season. Habitat suitability declined steadily after 450 mm water deficit, but the angle and extension of the slope to the right revealed that the complex will tolerate regions with decreased vegetation and increased dry seasons. Combined, the response curves suggest that understorey species will tolerate seasonal conditions, beyond established, evergreen forest cover.

The level of importance of individual drivers for threatened species complexes varies from one complex to another but the contribution of certain variables to the models for complexes is surprising (Table 2). For example, canopy height consistently contributed towards models for each complex (complex A: 23%; complex B: 17%; complex E: 35%), but the result for complex B is of particular interest. Complex B represents arboreal specialists and as such, we would superficially expect canopy height (model contribution = 17%) or EVI (model contribution = 13%) to be dominant drivers, instead the length and severity of the dry season (water deficit) had a greater influence on distribution (model contribution = 56%). However, arboreal species preferred regions of high moisture and short to no dry season as shown by the response curve to water deficit (Fig. 2c), both of which are predictors of evergreen forest. Arboreal species responded in a mostly linear way to canopy height; habitat suitability increased with greater canopy height, reaching a plateau of suitability at c. 40 m canopy height (Fig. 2a). As EVI increased to 0.46 (high vegetation cover) then so did habitat suitability for arboreal species, after which suitability dropped slightly and plateaued.

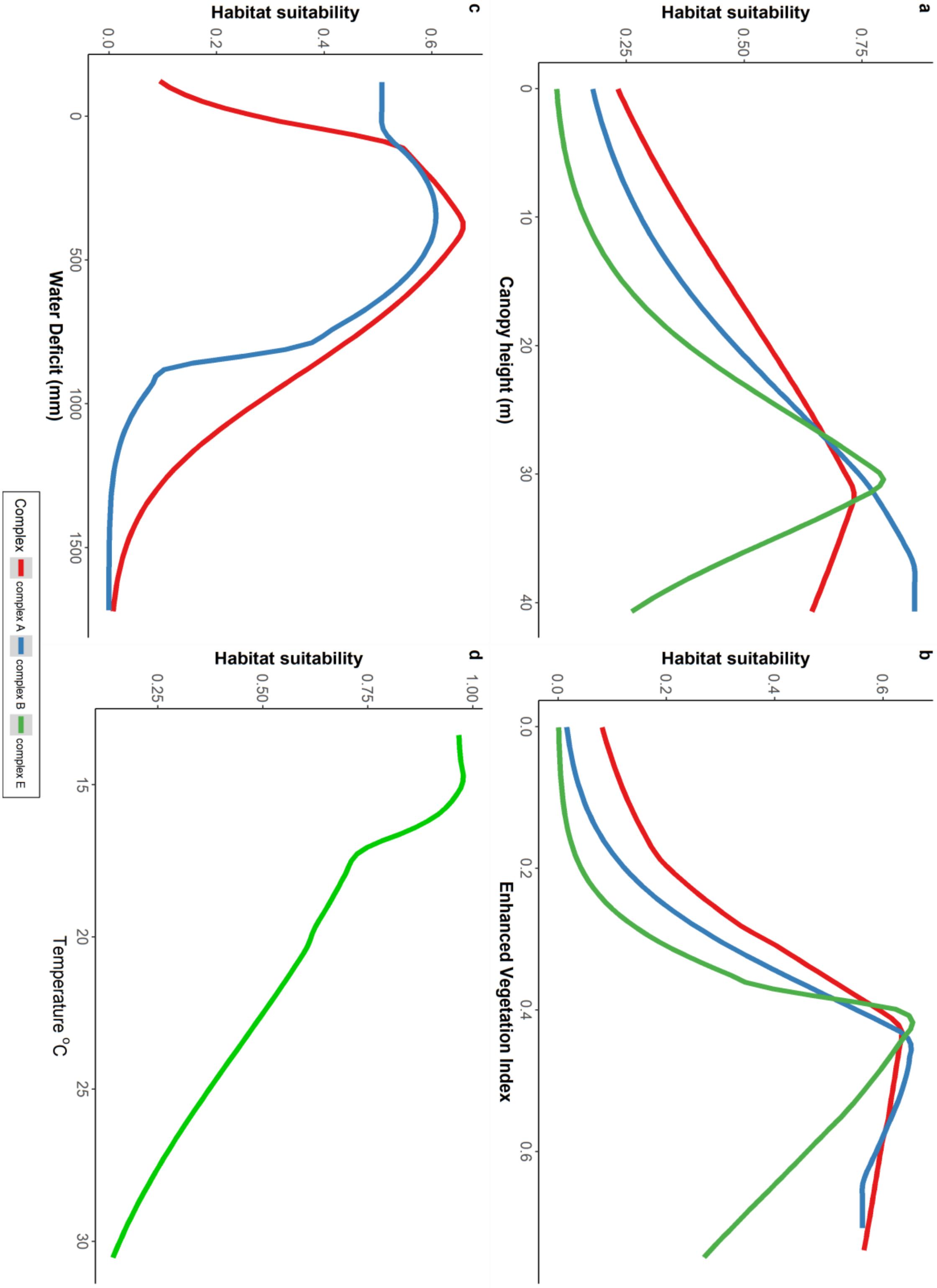
The response curves to water deficit, canopy height and EVI, all indicate that established evergreen forest is essential habitat for arboreal species.

Complex E (specialists) also gave interesting results; this complex's distribution was almost equally driven by canopy height (35%) and EVI (37%), but the temperature of the warmest quarter (16%) was unexpectedly more important than water deficit (2%). When only climate variables were considered for this complex, water deficit contributed 76% to the final model. Specialists responded to canopy height (Fig. 4a) with a peak of habitat suitability at 30 m, but habitat suitability (> 0.3) lay between a narrow range of canopy height (20 to 38 m). The complex also displayed a narrow band of habitat suitability for EVI which peaked at EVI = 0.4 and did not respond well to either too little vegetation/cover or too much (Fig. 4b). Further, habitat suitability for specialists is highest in regions where the temperature of the warmest quarter is below 20^{o}C (habitat suitability = c. 0.6) and higher still for temperatures below 17.5^{o}C (habitat suitability = c. 0.7). From the combined canopy height, EVI and temperature response curves, specialists preferred cool, temperate forest. Topographic wetness was expected to play an important role in describing the distribution of complexes, particularly for those complexes where breeding takes place water, but the variable was a poor predictor across models, contributing between 0.3% and 1.8% to the final models.

Table 2. Percentage contribution of habitat and climate variables to average MaxEnt models for trait complexes A, B and E. High contributing values to models are in bold. The importance of individual drivers to each complexes' model varies. Of interest is complex B (arboreal species) where the main driver is WD (56%) and not canopy height or EVI (17% and 13% respectively) as would be expected.

Variable	**Complex** **A**	 **B**	 **E**
Canopy height (CH)	**23.2**	**17.1**	**34.8**
Enhanced Vegetation Index (EVI)	**27.4**	**12.5**	**36.9**
Maximum water deficit (WD)	**18.5**	**55.6**	2.1
Mean temperature of the warmest quarter (TWQ)	5.4	7.9	**16.2**
Temperature seasonality (TS)	7.2	2.2	5.9
Rainfall wettest quarter (RWQ)	1.6	2.4	1.6
Topographic wetness index (TWI)	1.8	1.8	0.3
Topographic heterogeneity/terrain ruggedness index (THI)	1.8	0.5	2.1

Next page: *Fig. 4. The response of habitat suitability to the main drivers of distribution for trait complexes A, B and E.* ***a)*** *relationship between habitat suitability and canopy height. The response of complex A (understorey species) and B (arboreal species) to canopy height is predominately linear, with arboreal species requiring the greatest height in canopy. Complex E (habitat specialists) has a narrow band of habitat suitability (peak at c. 30 m canopy height).* ***b)*** *relationship between habitat suitability and Enhanced Vegetation Index (EVI). The response of all complexes suggests a reliance on vegetation cover. Again, complex E exhibits a narrow band of habitat suitability, with unsuitable habitat in either too sparse or too dense vegetation.* ***c)*** *complexes A and B respond to water deficit (WD) as the main climatic driver. Habitat suitability for arboreal species (complex B) is higher than complex A when WD is low, alluding that arboreal species can use regions with year-round moisture. But the sudden decrease of habitat suitability between 800 and 900 mm WD, indicates that complex B is not tolerant of extended dry seasons.* ***d)*** *The climate driver for complex E distribution, however, is the Mean temperature of the warmest quarter (TWQ). The complex prefers cooler regions.*


a
Habitat suitability
0.25
0.50
0.75
Canopy height (m)
0
10
20
30
40
b
Habitat suitability
0.0
0.2
0.4
0.6
Enhanced Vegetation Index
0.0
0.2
0.4
0.6
c
Habitat suitability
0.0
0.2
0.4
0.6
Water Deficit (mm)
0
500
1000
1500
d
Habitat suitability
0.25
0.50
0.75
1.00
Temperature °C
15
20
25
30
Complex
complex A
complex B
complex E

3.5 Discussion

The results demonstrate that inclusion of both habitat and climate variables adds important information in assessing distribution patterns of Malagasy amphibians, using TDMs. Climate TDMs potentially inform conservation through mapped outputs of suitable climate space, which can suggest species vulnerability to climate change (Chapter 2). Climate-only TDMs are sensitive, that is they will correctly identify component species of a trait complex because of the broader scale at which climate operates. However, species are reliant on both abiotic and biotic relationships in determining spatial patterns of distribution (Jiménez-Valverde, Lobo and Hortal, 2008); ecological processes and systems are considered scale dependent and hierarchical in structure (Cushman and McGarigal, 2002). Each level helps to define the distribution of resources, which in turn influence species distributions (Mackey and Lindenmayer, 2001), where climate is the primary filter (Keddy, 1992) and inside which habitat may be considered as an additional filter (Tonn *et al.*, 1990; Duflot *et al.*, 2014). Therefore, climate is a primary filter and many species share similar climatic conditions (Ackerly, 2003). As such, climate-only TDMs are not specific enough (true negative rate) and they over-predict trait distributions for habitat specialists.

Spatial over-prediction is minimal for habitat generalists as, by definition, they utilise a wide set of resources (both climatic and habitat). However, such species are normally less of conservation concern. Conversely to climate-only models, habitat-only models raise the specificity but do not change sensitivity. Although habitat is considered an additional ecological filter, models which incorporate only habitat variables perform worse than climate-only models, which may be because of the hierarchical nature of ecological systems and the interplay between the two levels (Thuiller, *et al*., 2004; Fournier *et al.*, 2017). We find that the climatic niche breadth is consistently narrower than the habitat-only niche breadth; overall amphibian distributions are climatically bounded (Buckley and Jetz, 2007). But by removing climatic constraints and considering habitat in isolation, the potential niche breadth is broadened. It is only when both layers of filtration, habitat and climate, are included together in the model structure do we see a significant increase in model performance and specificity, a result which is consistent with macroecological processes which shape species distributions (Barnagaud *et al.*, 2012). As species become more specialised in their resource use, then climate-only models increasingly over-predict distributions. Therefore, for TDMs to make meaningful conservation recommendations for specialists, often the focus of conservation, then habitat and climate must be considered together to fully understand the responses of trait complexes to the environment.

Habitat type and structure is an important consideration when deciding on management decisions for species, particularly of ectotherms (Bungard *et al.*, 2014). Specifically, vegetation character and structure appear to be crucial determinants of amphibian presence (Pineda and Halffter, 2004; Bastazini *et al.*, 2007; Müller *et al.*, 2013), often through provision of thermal and hydric refugia (Seebacher and Alford, 2002; Shoo *et al.*, 2011) which allows a mediated response to change in climatic character. For example, habitat may offer thermal buffering, allowing species persistence through expanded thermal or hydric (Nimmo *et al*., 2016) tolerances; old growth forest is effective in attenuating temperature (Norris *et al*., 2012, De Frenne *et al*., 2013), which may dampen the impact of climate change and create shelter microhabitats or microrefugia (Seebacher and Alford, 2002). Microrefugia can be either topographic, generated by physiographic processes (see Rull, 2009; Dobrowski, 2011) or habitat (biophysical processes), but both provide temporal protection for species under environmental change (Keppel *et al*., 2012). For species conservation, microrefugia are important because they can act as steppingstones between suitable habitat areas, facilitating species range shifts under climate change (Hannah *et al*., 2014, Keeley *et al*., 2018). But managing habitats for climate change will become a concern for amphibian species (Shoo *et al.*, 2011) particularly as many species will modify their dispersal movement under altered temperature and precipitation patterns, and matrix habitat may well become impermeable to amphibians (Guerry and Hunter Jr., 2002; Blaustein *et al.*, 2010). Further, the availability of water, an important component of amphibian lifecycles, varies between different habitat management strategies (Dietz *et al.*, 2006). In this study, topographic wetness should have been a reasonable predictor for the presence of some trait complexes. Despite being a poor predictor, topographic wetness is a valid variable for measuring amphibian occupancy of a grid cell. It is possible that the resolution (250 m) used in the models was too large relative to both size of amphibians and water bodies, which made this variable extraneous to the model; finer scales are needed for the relevance of this variable to be fully appreciated. In truth, the issue of scale is something that plagues identification of microrefugia within modelling frameworks (Lenoir *et al*., 2017) which requires very high-resolution data (Keeley *et al*., 2018) appropriate to the size of the species studied (Harvey and Weatherhead, 2006; Potter *et al.*, 2013). Variables at inappropriate scale will make interpretation of model results more difficult.

Amphibians utilise behavioural thermoregulation and evaporative cooling to modify their response to the surrounding environment (Tracy, 1976) and the effectiveness of response is linked to functional traits such as body size (Tracy *et al.*, 2010) and habitat preference. Therefore, within habitats some functional traits are more susceptible than others to increases in temperature (Scheffers *et al.*, 2013) often exemplified by amphibian's biphasic lifestyle. For example, direct developers were found to be more vulnerable than aquatic breeders as eggs were more sensitive to warming (Scheffers *et al.*, 2013). However, warming may well be analogous to increasing UV-B levels, to which for shade adapted species, exposure may be harmful (Middleton *et al.*, 2001). For many amphibian species, dispersal through the landscape to compensate for climatic shifts is also dependent on their functional traits, e.g. amphibians with aquatic larvae, specifically those in ponds and streams, rely on the integrity of landscape connectivity manifest as 'water connections' to provide the ability to traverse 'hostile' environmental patches (Becker *et al.*, 2010; Summers *et al.*, 2012). TDMs indicate broad scope management strategies for amphibians in differing habitats; for example, arboreal species are predominately distributed with evergreen forest, with a need for year-round moisture, but my results suggest that the forest needs to contain large trees, which suggests old growth/established forest. High-life living comes at a cost of greater exposure; arboreal ectotherms often use old growth trees because of the presence of micro-refugia which help to regulate thermal and hydric stasis (Bungard *et al.*, 2014) and in the case of arboreal amphibians, provide sites for egg deposition and act as a larval nursery (Andreone *et al*., 2007; Glaw and Vences, 2007). However, the role which proximal habitat plays in mediating water loss and how changing vegetation structure may then impact arboreal amphibian species, is unclear, but is likely to be related to distance and habitat type (Vallan, 2000; Watling and Braga, 2015). Therefore, other conservation measures may be required instead of or alongside habitat management. Because of their specialism and longevity of threat, threatened arboreal amphibians should make strong candidates for *ex-situ* management (Hannah, 2010; Tapley *et al.*, 2015) or translocation (Germano and Bishop, 2009; Hannah, 2010). Conversely, species within complex A (understorey species) can inhabit a range of vegetation habitats but still require canopy height, albeit not as tall as that for arboreal species, which suggests that secondary forest and some altered habitats, may still retain enough structural integrity to fulfil hydric strategies. Whilst species in complex E (habitat specialists) are mostly suited to temperate forests. A basic insight to be gained from TDMs is that we should avoid the assumption that intact primary forest is uniformly suitable (Ramiadantsoa *et al.*, 2015) for all trait combinations.

Simply restoring forest is perhaps an unrealistic goal for habitat management, particularly in Madagascar, where a rapidly growing human population has made such a significant impact on the landscape and heavy reliance is placed on environmental resources (Green and Sussman, 1990; Borgerson *et al.*, 2018). The financial burden of restoration and human impact of landscape use ultimately suggests that managed forest plots may provide a compromise for Madagascar (Hannah *et al.*, 2008). A managed model in which selectively harvested trees may provide local communities with sustainable resources whilst still maintaining both species diversity within the habitat and the required vegetative character (Banda *et al.*, 2006; Randriambanona *et al*., 2019). However, it will be important to differentiate between types of community forestry management, as is the case for Madagascar where variation in management practices has contributed to, not decreased, forest loss (Rasolofoson *et al*., 2015). Within managed habitats, where the aim is to off-set the financial cost of protection and restoration against community use, then we suggest that the plant species used need to be appropriate and carefully considered. For arboreal amphibians particularly, it is important to retain habitat structure, at least leaving core trees with the correct growth detail. However, Madagascar has a history of introduced vegetation where many species supply essential crops, medicines and wood fuel, which may help to alleviate demand on native forest (Kull *et al.*, 2012). In Madagascar, c. 9% of introduced plants are invasive and some, such as *Eucalyptus robusta,* are actively propagated for wood fuel covering an area of c. 180,000 ha (Kull *et al.*, 2012). But changes in the structure of vegetation such as tree density or degree of branching, can occur through introduced vegetation such as Ginger (*Zingiber officinale*) or Guava (*Psidium guajava*) and trees such as *Eucalyptus* spp (Rosa *et al.*, 2012; Tererai *et al.*, 2013; Bungard *et al.*, 2014). The problem with large scale propagation of introduced trees, is that they may not exhibit the same growth detail as native trees and alter availability of arboreal refugia (Whitford, 2002; Whitford and Williams, 2002) and structural attributes (Tererai *et al.*, 2013), potentially detrimental to semi-arboreal and arboreal species. To make matters worse, *Eucalyptus* presence in Madagascar has been shown to supress the growth of native seedlings and native forest regeneration (Baohanta *et al.*, 2012). Unfortunately, communal land-use can also significantly alter the structure and vegetative cover of lower habitat strata (Wessels *et al.*, 2011) which will also impact complex A (understorey) and E species (specialists). But where vegetative structure is maintained, there is evidence that amphibians will readily colonise revitalised habitat (Ruiz-Jaén and Aide, 2005). Furthermore, lessons from other taxa and agroforestry suggest that enhancing structural integrity can mitigate against climate change induced range contractions (Braunisch *et al.*, 2014) and retain biodiversity (Hemp 2005). Furthermore, evidence exists that despite intensive selective logging, tropical forests still demonstrate thermal buffering allowing microclimate refugia to persist (Senior *et al*., 2017).

3.5.1 Conclusions

This paper has examined whether inclusion of habitat variables improves TDM performance and the subsequent implications for habitat management for amphibians in Madagascar. The inclusion of habitat variables not only improved TDM performance but also provided an insight to community level habitat management in the context of Madagascar. TDMs which include habitat data give information on species (especially threatened ones) that would not otherwise be included in models (e.g. SDM) or would lack spatial outputs (e.g. Trait Based Assessments). The modelling framework and addition of habitat variables also suggest that such TDMs have a broad application across taxa and regions. Therefore, an assessment of functional traits should underpin habitat management strategies in conjunction with adaptive habitat management strategies (Millar *et al.*, 2007) which encompass ecological communities and thereby maximises diversity in the face of climate change. The rationale for such an assessment combined with adaptive management strategies is that vital conservation funds can be more effectively used; encompassing ecological communities will lead to a better chance of success for conserving biodiversity and biodiversity conservation will be better for people through livelihoods benefits – multiple wins. TDMs could conceivably form a component of Climate Change Integrated Conservation Strategies (CCS) (Hannah *et al.*, 2002; Midgley *et al.*, 2003) combining with fine-scale assessments to build empirical evidence which is relevant, accessible and useable for protected area management (Rafidimanantsoa *et al.*, 2018). Clearly there is plenty of scope for future research as Madagascar faces ongoing and rapid habitat loss (Ramiadantsoa *et al.*, 2015), potentially catastrophic shifts in climate (Tadross *et al.*, 2008) and rapid population growth and development (Gardner *et al.*, 2018). But within these threats, TDMs which combine habitat and climate variables can advise on combined climate and habitat strategies particularly for specialised species.

3.6 References

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Chapter 4. Trait Distribution Models suggest that amphibian conservation under future climate change is critical in lowland Madagascar

Preface

Climate and climate-influenced habitat controls amphibian distributions (Chapters 2 and 3). The climate vulnerability of tropical herpetofauna in Madagascar is significant (Raxworthy *et al.*, 2008), particularly through the combination of climate and land-use change that will impact acutely on amphibians in Madagascar (Nowakowski *et al.*, 2016). The ability of the protected area (PA) network to accommodate amphibian range shifts, or plan for the strategic siting of new PAs would be greatly improved by incorporating Climate Change Vulnerability Assessments (CCVA) that are spatially explicit. This chapter uses the framework developed across Chapters 2 and 3 to spatially assess 60 threatened Malagasy amphibians under predicted climate change and discusses the implications for the future impact of climate change on the Malagasy PA network in the context of amphibian losses.

This chapter is written in the style of *Conservation Biology*.

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4.1 Abstract

The climate vulnerability of amphibians in Madagascar is significant. Concern surrounds threatened species in vulnerable habitats and whether the protected area network in Madagascar can protect those species threatened by a changing climate. Here we used a Trait Distribution Model (TDM) framework to conduct Climate Change Vulnerability Assessments (CCVA) for data-poor, threatened Malagasy amphibians, and assess whether the protected area network safeguards species under predicted climate change for two end of century (2085) climate scenarios. Overall, 27 of the 60 threatened species assessed (45%) demonstrated high climate sensitivity, and eight species face extinction under a high emissions pathway (RCP8.5). Species with large altitudinal ranges have a lower climate sensitivity and decreased extinction risk, compared with species with narrower altitudinal ranges. Overall, Malagasy protected areas encompassed future species' ranges despite reductions in suitable habitat under predicted climate change, and therefore offer a level of safeguarding against climate change. However, protected areas in lowland zones are characterised by climate associated with future habitat loss and loss of threatened species, whilst highland zones (which are often perceived as threatened) are shown to be more resilient with no expected species loss and little reduction in habitat. Therefore, the most immediate challenges for conservation of amphibians in Madagascar are the protection of lowland species and formation of migratory corridors between protected areas in low and mid-altitudinal zones. On a broader scale, TDMs can potentially connect understanding from ecologists to habitat/conservation managers through their community approach.

Keywords: Climate Change Vulnerability Assessment, community ecology, protected areas, habitat management.

4.2 Introduction

Globally, amphibians are undergoing an extinction crisis (Stuart *et al.*, 2004; Wake and Vredenburg, 2008) driven by an interaction of threats from climate and land use change (Hof *et al.*, 2011) and yet conservation effort remains insufficient (Hoffmann *et al.*, 2010). Amphibians are highly climate sensitive due to their combined thermal and hydric reliance on the environment at different stages of their life history (Blaustein *et al.*, 2010; Lawler *et al.*, 2010) with future range shifts linked to this sensitivity (Chapter 2). Therefore, climate change presents a threat to amphibian survival, perhaps more so in regions with high amphibian diversity and specialism, such as Madagascar. Although no extinctions of Madagascar's amphibians have occurred to date, many species are threatened by other factors while also being considered climate vulnerable (Andreone *et al.*, 2008); shifts in the dry season could exacerbate existing pressures (Chapter 2).

Madagascar is a highly biodiverse Indian Ocean island with a distinct and mostly endemic assembly of flora and fauna (Goodman and Benstead, 2003). Amphibians (frogs, order Anura) are an important part of that biota and Madagascar is recognised for its amphibian species richness (Andreone *et al*., 2007; Andreone *et al.*, 2008). Numerous candidate species are being continually described (Vences and Glaw, 2005; Andreone *et al.*, 2008; Wollenberg *et al.*, 2008; Vieites *et al.*, 2009) and the numbers of described species have risen from 248 (in 2014) to over 300 endemic species (taxon reassessed, IUCN, 2017). Whilst rapid habitat loss in Madagascar (Harper *et al.*, 2007) is intensifying the level of threat for many species (Raxworthy and Nussbaum, 2000; Vallan, 2000), evidence suggests that the climate vulnerability of tropical herpetofauna in Madagascar is significant (Raxworthy *et al.*, 2008), particularly the combination of climate change and land use change that will impact acutely on frogs in Madagascar (Nowakowski *et al.*, 2016). Further still, Madagascar's human population is rising at c. 2.69% per year (World Population Review, 2019). Given this context of threats, the ability of the protected area (PA) network to accommodate amphibian range shifts, or plan for the strategic siting of new PAs would be greatly improved by incorporating Climate Change Vulnerability Assessments (CCVA) that are spatially explicit. Madagascar's climate is predicted to become warmer and wetter across the country but with longer dry seasons in the east (Hannah *et al.*, 2008; Tadross *et al.*, 2008; Platts *et al*., 2015). These climate shifts will particularly impact the biodiverse eastern rainforests (Hannah *et al.*, 2008), where most amphibian diversity is found (Andreone *et al.*, 2008), and consequently the future effectiveness of the PA network. However, the historical reasons for establishing PAs varies considerably, and as such they have enjoyed mixed levels of success in delivering conservation outcomes (Geldmann *et al.*, 2013), fuelling debate as to their overall effectiveness. This question has arisen due to the dynamic nature of ecology rather than the static snapshot which is often employed to determine PA location (Hole *et al.*, 2009), making the role of safeguarding highly questionable in the context of the impacts of climate change on species distributions.

If climate change is to be considered in evaluating the future effectiveness of PAs, then spatial planning should form an important component of the risk assessment process (Kujala *et al.*, 2013). Of concern, are threatened species in tropical montane habitat potentially shifting ranges upslope (Peters and Darling, 1985; Bentley *et al*., 2018) and specifically those which exhibit climate sensitive functional traits, such as arboreal specialists (Chapter 2). Therefore, spatial CCVAs are a key consideration in assessing PA function. PAs and their associated species would benefit from future proofing, that is either creating climate refuge areas, adjusting existing boundaries, or even considering the possibility of translocating species from one PA to another to track suitable future climate (Germano & Bishop 2009; Germano *et al*., 2015). Species Distribution Models (SDMs) are typically used to provide a spatially detailed CCVA, however, SDM performance deteriorates with few observations (n < 10) and as such, insufficient spatial data has proved to be a hurdle for many rare and threatened species, leading to their omittance from spatial CCVA (Platts *et al.*, 2014). To overcome the data hurdle, we conduct a CCVA of threatened amphibian species in Madagascar and assess the effectiveness of the Malagasy PA network, by using Trait Distribution Models (TDM; Chapters 2 and 3). We then used threatened species' climate sensitivities to evaluate whether Malagasy PAs safeguard threatened amphibians against predicted climate change.

4.3 Methods

4.3.1 Trait Distribution Model framework

A TDM framework (Chapter 2) was used to assess climate change vulnerability through measuring the response of multi-species groups based on species functional traits to four climatic and three habitat variables. As for previous chapters, the species baseline was derived from the 248 species in the IUCN Red List, 2014. The first step of the TDM framework, categorical ordination and K-means clustering of 248 Malagasy amphibian species, produced six complexes, of which three account for 88% (60 species) of threatened Malagasy amphibians (IUCN threat categories of vulnerable and above). CCVA was focussed on the threatened species in three complexes representing understorey species, arboreal species and habitat specialists.

4.3.2 Distribution modelling

MaxEnt v.3.3.3k (Phillips *et al*., 2006) was used to model distribution of complexes in Madagascar, under current and future climate conditions, through a combination of climate and habitat variables. Four climate variables were considered: mean temperature of the warmest quarter (^{0}C x 10; any consecutive three-month period); rainfall wettest quarter (mm; any consecutive three-month period); temperature seasonality (^{0}C x 10; standard deviation over monthly values) and Maximum water deficit (mm; consecutive months that experience rainfall < monthly Potential Evapotranspiration (Hargreaves method), over which the shortfall in rain is accumulated). Baseline climate conditions (1950-2000) were at a 30 arc-sec (c. 1 km) resolution and derived from WorldClim (Hijmans *et al.*, 2005). For future climate scenarios, two end-of-century (2085), Representative Concentration Pathways (RCP4.5 and RCP8.5) of the Intergovernmental Panel on Climate Change's Fifth Assessment Report (IPCC-AR5) (IPCC, 2013) were used. Three habitat variables were also considered: Enhanced Vegetation Index (EVI; higher values refer to abundant vegetation); topographic heterogeneity/terrain ruggedness index (high values are a measure of a variable landscape) and canopy height (m) (Simard *et al.*, 2011; ORNL DAAC, 2017). Forecasting the way climate change influences canopy height and EVI is difficult to model. To partially account for the interaction between climate and vegetation structure, we modelled canopy height and EVI with climatic variables and viewed how these two variables change with the future climate (Vieilledent, pers. comm). We extracted values and coordinates from canopy height and EVI rasters, then modelled these against current and future climate conditions across the extent of Madagascar. By doing so, we produced rasters for use in distribution modelling which assume no change in the vegetation values in the future. However, such rasters do indicate the marginal effect of climate change on habitat variables through changes in the values of climatic variables (Vieilledent *et al.*, 2016). Model resolution was set at 250 m, therefore climate variables (1 km) were interpolated to the finer resolution using bilinear interpolation (weighted distance average) in ArcGIS 10.3.1 (ESRI, 2015). To analyse raster data, the packages rgdal (Bivand *et al*., 2018) and raster (Hijmans, 2017) in R for windows, v. 3.5.0 (R Core Team, 2018) were used.

MaxEnt settings were modified from the default settings as follows. All models were cross-validated 10 times and to determine variable importance within models, climate and habitat data were jack-knifed. Models were debiased by a kernel density derived from amphibian sightings across Madagascar (Fourcade *et al.*, 2014) and the regularisation (β) coefficient was adjusted to reduce over-fitting (Warren *et al.*, 2010; Warren and Seifert, 2011). Model performance for cross validated models was assessed by the mean Area Under the Curve (AUC) statistic and True Skills Statistic (TSS) (Liu *et al.*, 2005). Current and future trait-complex distributions were transformed from continuous predictions of suitability into presence-absence classes using the Maximum sensitivity plus specificity logistic threshold (Liu *et al.*, 2005; Liu *et al*., 2016) to balance the errors and give presence-absence estimates.

4.3.3 Climate change vulnerability assessment

For each species of interest (Table S1), climate sensitivity was calculated by overlaying a 10 km buffered IUCN Minimum Convex Polygon (MCP; IUCN, 2014) on current and future trait complex distributions. A 10 km buffer was used as a reasonable approximation to account for potential maximum species dispersal (Smith and Green, 2005). Climate sensitivity per species (S_{is}) was calculated by the proportional change in suitable habitat (number of grid cells; Equation 1).

Equation 1

$$S_{is} = \left(\frac{\sum_{k=1}^{m} LCc_{ik} - LCh_{ik}}{\sum_{k=1}^{m} LCc_{ik}}\right)$$

The equation accounts for change in the number of grid cells occupied (m); where, the number of suitable grid cells for climate change layer (LCh_{ik}) is subtracted from suitable grid cells in the current climate layer (LCc_{ik}), over the current climate layer (LCc_{ik}). Species where $S_{is} = 1$ show high sensitivity (i.e. high extinction risk) and where $S_{is} = -1$, low extinction risk. A generalised linear mixed model (GLMM) was built to analyse the relationship between S_{is} and distributional range and traits. Species' range size (total number of grid cells), body size (snout-vent-length, mm), habitat tolerance (number of occupied habitat types) and altitudinal range (m) were entered as fixed effects. Trait complex and climate scenario were treated as random effects. Residual plots were inspected for deviations from homoscedasticity and normality. Non-significant terms were removed from the model and at each step, models were assessed using conditional Akaike's Information Criterion (cAIC) (Säfken *et al.*, 2018). Variance explained for fixed factors only is presented as marginal R^2 and for both random and fixed factors as conditional R^2 to explain the combined impact of random and fixed factors (Nakagawa and Schielzeth, 2013). Data were analysed with R (R Core Team, 2018) and packages used were: lme4 (Bates *et al.*, 2015) to perform the GLMM, MuMIn to obtain marginal and conditional R^2 (Barton, 2018) and cAIC4 to obtain cAIC (Säfken and Ruegamer, 2018).

4.3.4 Assessment of protected areas

We assessed how well the PA system in Madagascar (UNEP-WCMC and IUCN, 2018) accounted for threatened amphibians from their individual species trait distributions. For each species (i) and climate scenario (s), the percentage of range within protected areas (effectiveness, Ef_{is}) was determined by a simple calculation of $PA_{ik}/Tcell_{ik}$ x 100. We calculated the total number of grid cells of suitable habitat ($Tcell_{ik}$) within respective buffered IUCN minimum convex polygon and then, by overlaying the protected area network for Madagascar, the number of grid cells of suitable habitat within protected areas (PA_{ik}).

To see whether PA effectiveness changed with climate scenarios, differences in Ef_{is} between each climate scenario were calculated by repeated measures ANOVA, as Ef_{is} data were normally distributed. Changes in total suitable habitat ($Tcell_{ik}$) and in suitable habitat in protected areas (PA_{ik}) between climate scenarios were assessed through non-parametric Friedman tests, followed by Nemenyi post hoc tests (Pohlert, 2014) on significant results. The mean altitude (m) of each Malagasy PA was calculated and grouped into low (0 – 799 m), medium (800 – 1400 m) and high altitude (> 1400 m) zones to see whether species loss and changes in suitable habitat varied with PA altitude under predicted climate change. Differences between zones were assessed by Kruskal-Wallis test, followed by pair-wise Mann-Whitney U tests on significant results. In all statistical tests, $\alpha = 0.05$, two-tailed.

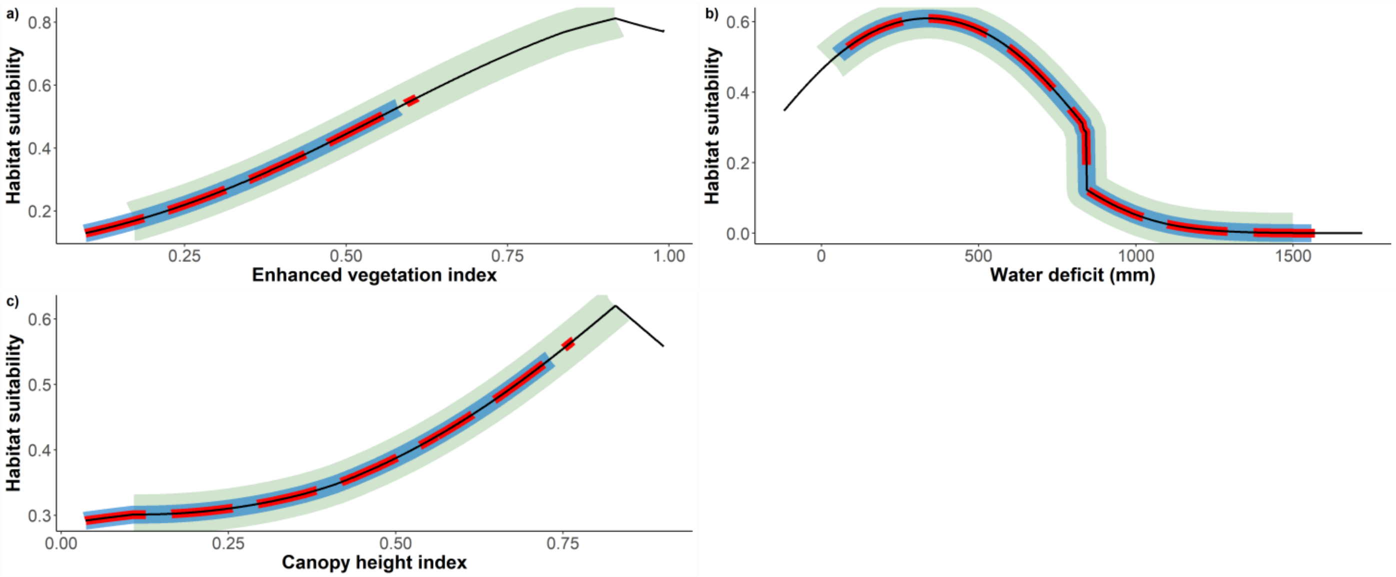
4.4 Results

4.4.1 Drivers of distribution

Under current climate conditions, trait complexes showed strong correlation to environmental variables but differed in the importance attributed to the primary drivers of distribution; these were EVI (understorey species; 54% contribution to the final model), water deficit (arboreal species; 38% contribution) and canopy height (specialists; 38% contribution). Changes in habitat suitability to primary drivers were evident from the response curves of each complex (Fig. 1). Understorey species (complex A) demonstrated a mostly linear response to EVI, whereas arboreal species exhibited a gamma-shaped response to water deficit (Fig. 1a and b) and habitat suitability for specialists was driven by canopy height. Habitat suitability for specialists increased up to a canopy height of 32 m, after which suitability sharply declined (Fig. 1c). From the response curves it can be summarised that understorey species and specialists' distributions are largely determined by vegetative cover, however the distribution of arboreal species (complex B) is determined mostly by changes in the length and severity of the dry season (water deficit). Such a result for arboreal species is unexpected, as logically a group that is dependent on vegetation should respond to changes canopy height/EVI. However, the length and severity of the dry season may better characterise vegetative structure as water deficit affects physiological and morphological characteristics of plants (Luvaha *et al.*, 2008).

Two scenarios for end-of-the-century climate change (2085; RCP4.5 and RCP8.5) were considered, both of which affected the distributions of complexes by decreasing habitat suitability in response to the primary drivers of EVI (understorey species), water deficit (arboreal species) and canopy height (specialists).

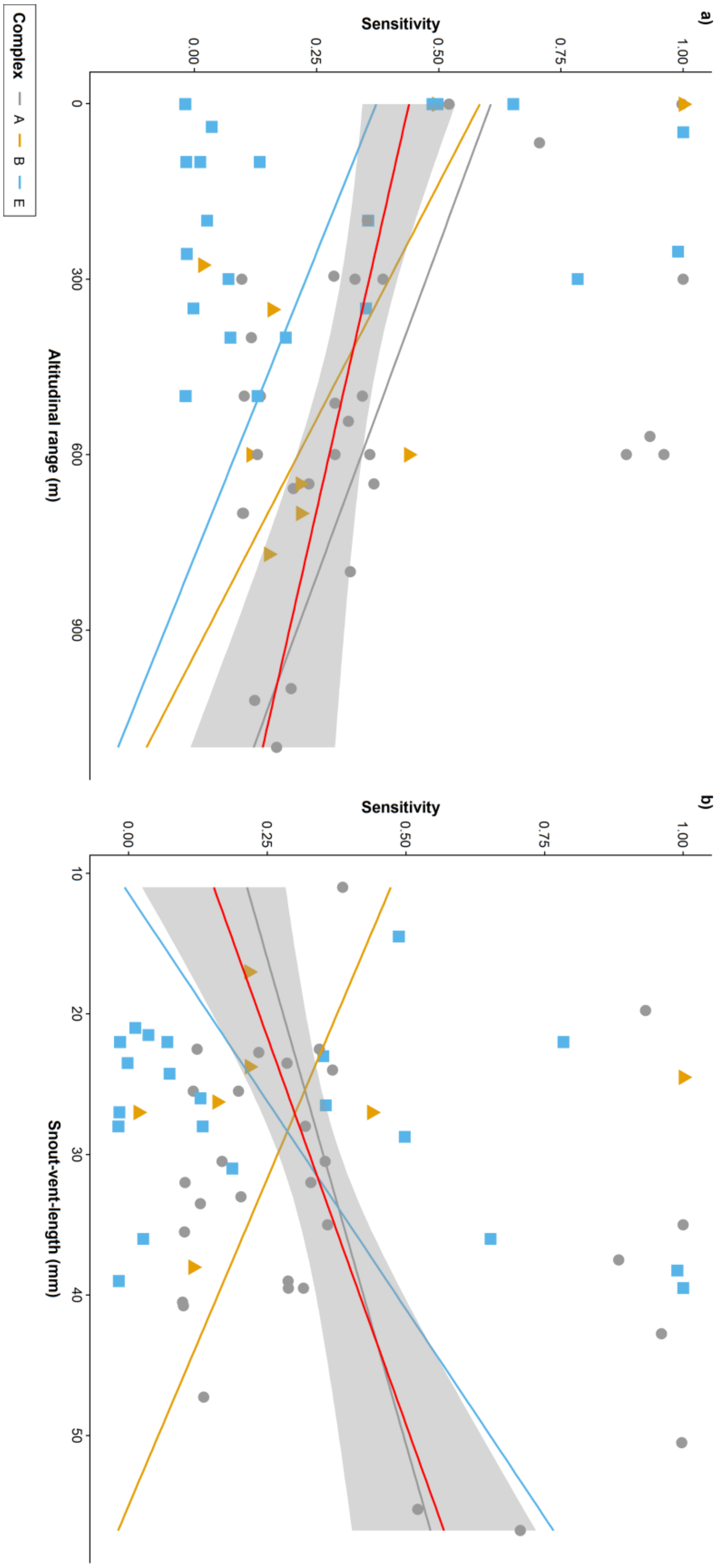
Fig. 1. Response of threatened species' trait complexes understorey species, arboreal species and habitat specialists to primary drivers of distribution for current climate and two end-of-century scenarios (RCP4.5 and RCP8.5). Each trait complex is strongly correlated to one of three drivers: Enhanced Vegetation Index (EVI), water deficit (WD) and canopy height. The black lines show the variation of habitat suitability against each driver. The range of each driver is shown for current climate (thick green line), RCP4.5 (blue line) and RCP8.5 (long dashed red line). General trends suggest that habitat suitability decreases under future climate scenarios for all complexes as the primary drivers become constrained across ranges. ***a)*** *Habitat suitability for understorey species increases as EVI increases, suggesting a preference for forest cover. Under both climate scenarios there is a reduction across the complex' s range of EVI and therefore habitat suitability.* ***b)*** *Arboreal species are driven by changes in WD, with minimal tolerance to dry conditions (habitat suitability decreases where WD > 800 mm). The range of WD under future conditions shows a shift to the right and indicates a drier climate with lower habitat suitability.* ***c)*** *Habitat suitability for habitat specialists increases with canopy height to an index of 0.8 (equivalent to c. 32 m) after which there is a rapid decline in suitability.*



4.4.2 Climate change vulnerability assessment

The results of the GLMM suggest that climate sensitivity for threatened species is dependent on altitudinal range ($F_{1,\,88}$ = 11.087, p = 0.001) and snout-vent-length, although the affect snout-vent-length had upon the final model is less than altitudinal range ($F_{1,\,106}$ = 3.337, p = 0.070, 95% CI [0.004, 0.013]). The cAIC improved from 52.21 for the primary model to 48.21 for the final model. Where climate sensitivity = 1, there is an increased extinction risk from loss of range; the final model showed that increasing altitudinal range lowered sensitivity by -0.00038, ±0.00016 (SE) (Fig. 2a): for each meter increase in altitudinal range, species' extinction risk decreased by 0.00038. Therefore, species with large altitudinal ranges had a lower climate sensitivity and decreased extinction risk and species with narrow altitudinal range tended to be more climate sensitive. Overall, larger body size (snout-vent-length) increased sensitivity by 0.005 ±0.003SE per mm body size (Fig. 2b). However, the relationship between sensitivity and snout-vent-length differed for species in each complex; both understorey species and specialists demonstrated increasing climate sensitivity with increasing size, whilst for arboreal species sensitivity decreased as size increased. The dependency of climate sensitivity on fixed factors (altitudinal range and snout-vent-length) is weak. The proportion of variance explained by the fixed factors was 14% (marginal R^2), whilst the proportion of the variance explained by both fixed and random factors was 22.7% (conditional R^2). The conditional R^2 suggests that trait complex and climate scenario have an influence on altitudinal range and svl than can be explained by altitudinal range and svl alone.

Next page: *Fig. 2. The relationship between threatened species' climate sensitivity index for two end-of-century (2085) Representative Concentration Pathways (RCP4.5 and 8.5) and generalised linear mixed model (GLMM) variables. In each plot, the red line shows the population response of the model (Standard error is shown as grey shading) and slopes for species in individual complexes A (understorey species), B (arboreal species) and E (specialists) are coloured grey, gold and blue respectively.* ***a)*** *climate sensitivity is negatively related to altitudinal range. Narrow ranging species are more climate sensitive than wider ranging species.* ***b)*** *Climate sensitivity also varies in response to body size (snout-vent-length) depending on complex; larger arboreal species in complex B show decreased climate sensitivity, the opposite of understorey species and specialists.*


a)
Sensitivity
0.00
0.25
0.50
0.75
1.00
0
300
600
900
Altitudinal range (m)
b)
Sensitivity
0.00
0.25
0.50
0.75
1.00
10
20
30
40
50
Snout-vent-length (mm)
Complex
A
B
E

4.4.3 Assessment of protected areas

Of the 60 threatened Malagasy species that were considered (Table S1), 20% (12 species) were highly climate sensitive (i.e. $S_{is} > 0.5$) with five species (*Aglyptodactylus laticeps*, *Boophis tampoka*, *Cophyla berara*, *Gephyromantis azzurrae* and *Scaphiophryne gottlebei*) projected to face extinction under RCP4.5 by 2085. The number of affected species increased under RCP8.5; 45% (27 species) were highly climate sensitive with eight species (*Aglyptodactylus laticeps*, *Anodonthyla vallani*, *Boophis tampoka*, *Cophyla berara*, *Gephyromantis azzurrae*, *Gephyromantis corvus*, *Scaphiophryne gottlebei* and *Scaphiophryne menabensis*) projected to lose all habitat suitability by the end of the century. Two species, *Aglyptodactylus laticeps* and *Scaphiophryne menabensis*, have previously been identified as high risk due to habitat loss and have been recommended for long-term monitoring (Glos *et al.*, 2008). Under RCP4.5 and RCP8.5 there were significant decreases in both total suitable habitat ($Tcell_{ik}$; $\chi^2 = 60.941$, df = 2, $p < 0.001$) and suitable habitat within protected areas (PA_{ik}, $\chi^2 = 93.576$, df = 2, $p < 0.001$; Fig. 3b and c) when compared to current climate. However, PAs in Madagascar encompass species ranges despite reductions in suitable habitat under predicted climate change. In fact, the overall effectiveness of PAs remained static, with no significant change under climate change and any projected range shifts that occurred are into PAs, not out of them. The ability of the Malagasy PA network to account for range shifts is possibly related to sheer size. The network covers 72,816 km^2 or c. 12% of Madagascar and is mostly located in the biodiverse eastern side of the country, with PAs dominating low and mid altitudinal regions (Fig. 4a). Nevertheless, species losses are projected to be significant regardless of climate scenario when PAs are grouped into low, medium and high-altitude zones (RCP4.5, $\chi^2 = 8.637$, df = 2, $p = 0.013$; RCP8.5, $\chi^2 = 11.274$, df = 2, $p = 0.003$). The number of threatened species in PAs is greater in mid-altitudinal PAs ($\bar{x} = 5$, SD = ± 2) when compared to low altitude ($\bar{x} = 2$, SD = ± 2) PAs (W = 510, $p < 0.0001$). However, we found that the percentage of threatened species losses were significant in low altitude parks (RCP4.5, W = 366, $p = 0.009$; RCP8.5, W = 386, $p = 0.003$), where most Malagasy PAs are concentrated, with fewer losses in mid-altitudinal zones and none in high altitudes (Fig. 4b). Habitat loss in lowland PAs is significant under both scenarios when compared to mid- and high-altitude zones (RCP4.5, $\chi^2 = 10.539$, df = 2, $p = 0.005$; RCP8.5 $\chi^2 = 12.25$, df = 2, $p = 0.002$; Fig. 4c), typically around 55% for both climate scenarios.

Fig.3. Impact of climate change on the availability of suitable habitat for threatened species (understorey, arboreal and specialist complexes) in protected areas. ***a)*** *The total amount of suitable habitat (number of grid cells) for threatened species of understorey, arboreal and habitat specialist complexes in each protected area under current climate conditions. Subsequent loss of habitat is shown as a percentage decrease in each protected area, for two 2085 scenarios;* ***b)*** *RCP4.5 and* ***c)*** *RCP8.5.*

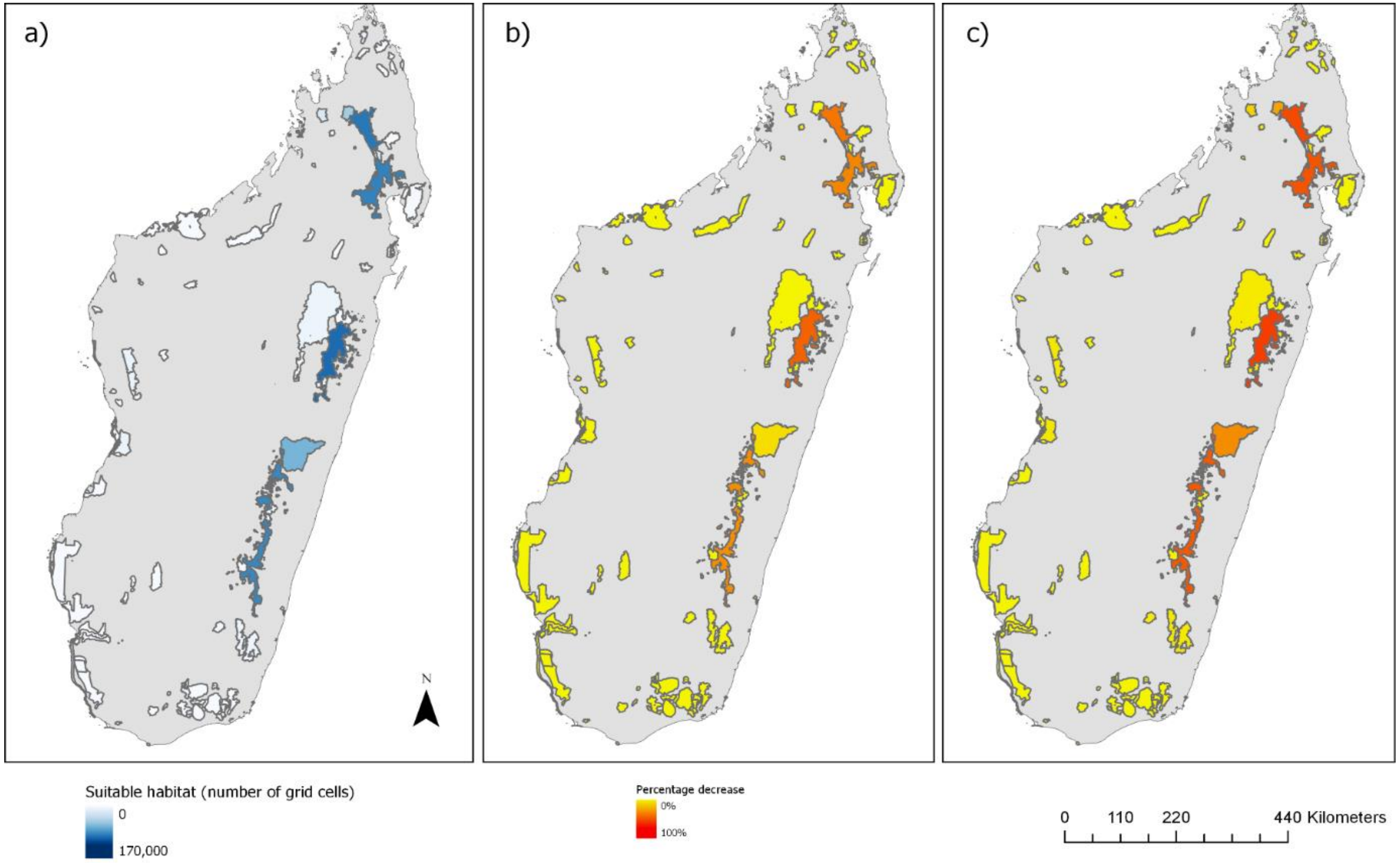
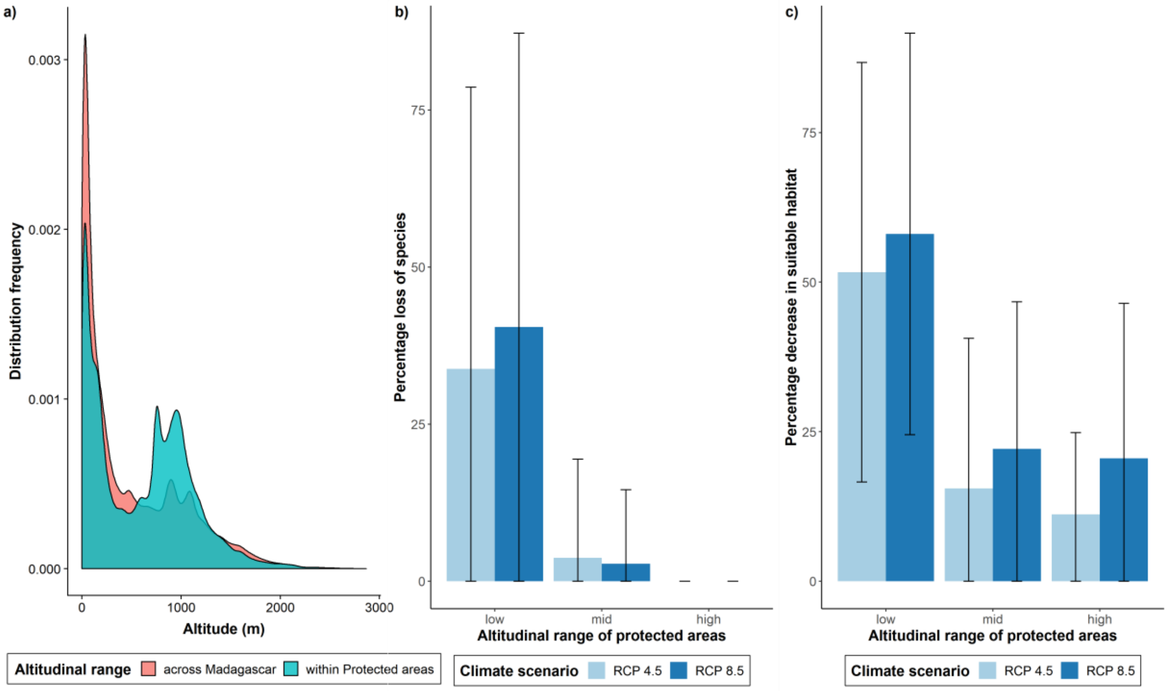


Fig. 4. The impact of climate change on suitable habitat and amphibian species numbers in Malagasy protected areas (PA) in low (0 – 799 m), mid (800 – 1400 m) and high (> 1400 m) altitudinal zones. ***a)*** *Malagasy PAs are concentrated around the low to mid-altitudinal range, where mid-altitudinal concentration is more than the observed spread of range of altitude over Madagascar.* ***b)*** *Percentage loss of threatened species in PAs in low, mid and high-altitude zones for climate change scenarios RCP4.5 and RCP8.5. Species loss is highest in low altitudinal zones, with no expected losses in high altitude zones.* ***c)*** *Percentage decrease of suitable habitat in PAs for predicted climate change (RCP4.5 and 8.5) across altitudinal zones. Decrease of suitable habitat is greatest for low altitude PAs regardless of climate scenario. In both* ***b*** *and* ***c****, error bars show standard deviation.*



4.5 Discussion

There are global concerns for climate driven attrition of biota across tropical lowlands (Colwell *et al.*, 2008) and the results presented here supports these concerns. The results suggest that for threatened Malagasy amphibians, lowland PAs are imperilled (Ganzhorn *et al.*, 2001), facing both species and habitat loss under climate change. Furthermore, the data also suggest that although habitat suitability will decline in mid and high altitudinal zones, that species losses in these areas will be relatively low. Therefore, threatened species losses in combination with decreases in suitable habitat suggests that mid-altitudinal zones and highland PAs, may be more resilient to climate change than lowland regions. Amphibian presence in the environment is driven by the interaction between temperature, precipitation and vegetation, where vegetation creates microhabitat that attenuates climate impacts (Seebacher and Alford, 2002). Future rainfall patterns in Madagascar are projected to alter, particularly in seasonal rainfall along the East coast with prolonged dry seasons (Tadross *et al.*, 2008). The extended seasonal drying of the environment and increase in temperature will alter vegetation composition and structure (Vieilledent *et al.*, 2016) which will negatively impact amphibian persistence in lowland zones. Predominately, vegetation structure will adversely impact amphibians distributions through a predicted decrease in average tree size and changes in tree species distributions (Vieilledent *et al.*, 2016). Furthermore, seasonal shifts in rainfall patterns will also alter breeding cues for many species, changing phenology, a phenomenon that has already been observed in other taxa and regions (Walther *et al.*, 2002). The loss of lowland habitat will place a greater emphasis on highland topographic/habitat refugia as amphibian strongholds, but we suggest pushes lowland regions to the fore to receive sustained conservation effort.

Strategies for amphibian conservation in Madagascar, such as control of harvesting for trade, engaging stakeholders in conservation, *ex-situ* capacity development, developing monitoring capacity within Madagascar and climate change research, are provided by the national strategy for conservation: A Conservation Strategy for the Amphibians of Madagascar (ACSAM; Andreone and Randriamahazo, 2008; Andreone *et al.*, 2016). However, despite urgency (Andreone *et al.*, 2008) and being a targeted action within the ACSAM (Andreone and Randriamahazo, 2008), little progress has been made in identifying the climate vulnerability of Malagasy amphibians (Andreone *et al.*, 2016). There are possibly two good reasons for this lack of progress; 1) countrywide assessment of amphibians is logistically difficult (D'Cruze *et al*., 2009) and 2) in terms of a triage approach to conservation, habitat loss is a more immediate threat to amphibian survival (Gascon *et al.*, 2007).

From our data, climate-driven habitat loss may imperil some trait complexes more than others. Amphibian response to the environment is controlled by an interplay between body size and cutaneous resistance which influence physiological performance (Tracy *et al*., 2010) and in turn dictates choice of microhabitat (Köhler *et al.*, 2011). Typically, arboreal species have a high cutaneous resistance (an adaptation to arboreality) allowing them to bask. For small species, basking confers an ability to rapidly elevate body temperature and therefore improved locomotor performance (Tracy *et al*., 2010). However, basking increases exposure and may in part explain why small, arboreal species demonstrate higher sensitivity in our models. Indeed, the distribution of arboreal species is constrained by a drier climate and corresponding changes in vegetative cover. Alternatively, standing leaf litter is a critical microhabitat choice for more terrestrial species (Edwards *et al.*, 2019) and climate driven declines in the quantity/depth will impact the hydric stasis of amphibians through restricted microhabitat choice (Whitfield *et al.*, 2007). The distribution of terrestrially orientated complexes in Madagascar are mostly driven by established forest and it is possible that declines in leaf litter depth will leave larger species more exposed, exasperating their vulnerability. The distribution models for understorey species points towards management strategies for PAs and corridors that retain vegetative structure to help fulfil microhabitat requirements.

As climate changes there is an inevitable shift in land-use which in turn alters vegetative structure (Brown *et al.*, 2015). For example, shifts in Madagascar's recent climate have prompted an alteration in the character of agriculture, from cultivation of rice to rain-fed crops such as maize and groundnuts, produced from slash-and-burn shifting agriculture (Tavy) of forests (Waeber *et al.*, 2015). Whether the shift in agricultural patterns is directly connected to a changing climate (e.g. better yield under warmer/drier conditions) or whether it is linked indirectly to climate through changing economic opportunities, or a combination of both, (Lambin *et al.*, 2001; Lambin *et al.*, 2003), is hard to attribute, but a climate-led shift in land-use fundamentally changes habitat structure leading to habitat loss. It is likely that climate-induced land-use change will accelerate species extinction and will certainly increase vulnerability, creating a synergistic effect whereby climate drives both land-use change and direct habitat loss. Therefore, whilst there is no doubt that prioritisation is essential to preserve species (e.g. habitat protection), at least one eye needs to be on the future to safe-guard current conservation efforts (e.g. PA establishment and management) against changes in land-use, without conceding to significant mitigation costs (Busch *et al.*, 2012) and future species survival.

An ideal rationale behind protected areas establishment is that they should 1) represent the biodiversity of a region and 2) safeguard biodiversity against threats (Margules and Pressey, 2000). But these rationales require flexibility of both boundaries and management strategies in response to changing targets. In truth, PAs can be considered as a static snapshot of conservation (Hole *et al.*, 2009); they are typically set up with a defined role, which changes over time (Naughton-Treves *et al*., 2005). Whilst the role changes, the boundaries often remain the same. Although Madagascar has seen a rapid expansion in its PA network since 2003 (Gardner *et al.*, 2018), the status of PA does not necessarily alleviate pressure on local ecosystems. Malagasy PAs vary in their management effectiveness, across ecosystems and taxa, which means that the operative area protected is far less than the areal extent of the PA network (UNEP-WCMC, 2019). There is substantial socio-economic pressure on Madagascar's environment, notably on forest blocks, through over-harvesting of resources from a growing yet impoverished population (Waeber *et al.*, 2015; Borgerson *et al.*, 2018; Gardner *et al.*, 2018) and especially where the previously conservative taboo system is being eroded due to exposure to modern living (Jones *et al*., 2008). It seems of no coincidence that the most rapid deforestation has occurred in areas of low elevation with high population density (Green and Sussman, 1990). However, deforestation may not be directly linked to human population levels (McConnell, 2002; Rogers *et al.*, 2010) and more intrinsically linked to land security (Elmqvist *et al.*, 2007; Virah-Sawmy, 2009). Regardless of cause, low elevation deforestation coupled with our projections of climate-associated species and habitat loss, makes lowland zones a conservation priority.

If we simply look at the ability of Madagascar's protected areas to encompass changes to amphibian species ranges under climate change, then for most species, they are effectively placed. Previously the PA system offered protection to 82% of threatened amphibians (Andreone *et al.*, 2005). The complexities behind the establishment of Madagascar's PAs (Gardner *et al.*, 2018) suggest that the representation of threatened amphibian species in the country's PA system is coincidental and not specifically targeted (Kremen *et al.*, 2008). Yet amphibian species with contracting ranges under climate change still fall or shift inside park boundaries. But our models and assessments do not include any detail regarding edge effects; the radius of effect produced by changes in land-use and from other forms of anthropogenic disturbance, nor do they speak of broader measures of park effectiveness (Naughton-Treves *et al*., 2005). Therefore, amphibian species ranges may well receive some protection under projected climate change, but the overspill of impact from the surrounding matrix beyond park boundaries may reduce the effectiveness of protection. A simplistic solution would be to extend park boundaries where needed, but such a move would be potentially exclusionist and would not incorporate livelihood benefits. Nor does the extension of boundaries acknowledge the clustering of human populations around parks because of perceived resource availability (Pfeifer *et al.*, 2012). We certainly recognise the complexity surrounding PA management in Madagascar and the difficulties in enhancing local participation, achieving financial stability and sustainable resource-use (Gardner *et al.*, 2018). However, layered management systems whereby the area within the park and surrounding area are subjected to different management options and techniques to control the impact of anthropogenic activity, may be an effective choice. Such layering would help to promote the environmental agenda beyond park boundaries (Naughton-Treves *et al*., 2005) and community ecology approaches such as TDMs may give park managers a more targeted approach to management, rather than species specific. A community ecology approach may hold wider benefit to safeguarding ecosystem services as amphibians are indicators of ecosystem health (Nori *et al.*, 2015).

However, at a species level within the PA network, the combination of specific trait characteristics highlights some species as priorities for conservation. Species sensitivity to climate is linked to altitudinal range and body size, with the latter inversely changing depending on complex. Thus, large bodied, narrow ranging terrestrially orientated species should be of concern, whilst narrow ranging, small bodied arboreal specialists should be considered as conservation important. This detail combined with the results of distribution models for the complexes, indicates that management practices for corridors and PAs which maintain or restore vegetative structure, not necessarily the composition of plant species, under climate change would be advantageous. The number of recognised frog species in Madagascar has substantially increased in recent years

(Vieites *et al.*, 2009; Ludwig-Maximilians-Universität, 2020), with many new species lacking substantial detail regarding population levels. Based on our results, we suggest that those newly recognised arboreal species with narrow altitudinal ranges should be considered highly climate sensitive.

Overall, we predict that eight threatened species will be lost under climate change, although this is likely to be a conservative estimate as models focus on climate-derived variables only (Hof *et al.*, 2011) and not from anthropogenic impact from land-use changes driven by climate. Land-use changes will undoubtedly accelerate climate-associated extinction rates for amphibians (Rogers *et al.*, 2010; Nowakowski *et al.*, 2016). Furthermore, the synergistic effect between climate, land-use and emergent diseases, notably *Batrachochytrium dendrobatidis* and Ranaviruses (Blaustein *et al.*, 2012; Price *et al.*, 2014), will place pressure on threatened species (Hof *et al.*, 2011). Amphibian susceptibility to pathogens such as *Batrachochytrium dendrobatidis* is complex but linked to host stress levels and modes of transmission (Blaustein *et al.*, 2012). The transmission of amphibian pathogens is connected to precipitation and temperature gradients and host stress levels are intensified by both temperature/precipitation changes and changes in habitat (Blaustein *et al.*, 2012). Plausibly, species which already demonstrate high levels of sensitivity to climate change are more likely to be adversely affected by additional threats, raising the number of extinctions. Nor did we explicitly model for time lags, the impact of changes in population dynamics induced by climate change, which will invariably add to the extinction rate (Fordham *et al*., 2016). As a methodology, TDMs are not prescriptive in determining actual range shifts, however TDMs are a pragmatic framework which allows researchers to identify which data-poor species may exhibit range shifts under climate change. Unfortunately, there is little evidence that spatial responses to climate change are considered for decision making in PAs (Guisan *et al.*, 2013), and there are distinct issues with research results being disseminated to park managers (Rafidimanantsoa *et al.*, 2018), which need to be overcome. However, we urge that CCVA are more regularly incorporated into planning and management decisions and we strongly recommend that any climate sensitive species are subjected to further data collection which meets the assumptions of the chosen species distribution model. For predicted climate change, we recommend three broad management priorities for amphibian conservation in Madagascar. Firstly, an improved focus on habitat protection in lowland PAs and an increase in available corridors/connectivity to higher altitudes. Secondly, prioritisation of habitat management techniques that favour narrow ranging, small, arboreal specialists and large, terrestrially orientated species. Specifically, retention or planting of structurally suitable trees to create canopy height and thinning of areas of secondary growth. Additionally, such species could be considered for *ex-situ* management (Tapley *et al.*, 2015). Thirdly, the use of techniques which retain vegetative structure and thereby promote wider ecosystem services. Retention of ecosystem services coupled with sustainable use of land surrounding PAs, will help support amphibian population longevity as well as conservation of other taxa. On a global scale, the ability of TDMs to review the broader ecology of a region allows TDMs to assess multiple species and ecosystem services (the benefits of nature for people). Spatial assessment of ecosystem services has been limited and conservation decisions in Madagascar have been supported by biodiversity data, not ecosystems services data (Neugarten *et al*., 2016). Therefore, ultimately, we put forward TDMs as an ecological approach to PA management in the face of increasing challenges from climate change.

4.6 References

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4.7 Supplementary

Table S1. Threatened Malagasy amphibian species (IUCN, 2014) and their climate sensitivity (S_{is}) under two end-of-century (2085), Representative Concentration Pathways (RCP4.5 and RCP8.5) of the Intergovernmental Panel on Climate Change's Fifth Assessment Report (IPCC-AR5). Highly climate sensitive species (S_{is}> 0.5) are highlighted in bold for each scenario. Species which face extinction (S_{is} > 0.99) are also starred. As climate pathways are progressive (the conditions of RCP4.5 will be met before RCP8.5), then extinction risk under RCP4.5 is assumed for RCP8.5.

Species	IUCN threat category	Climate change sensitivity (S_{is})	
		RCP4.5	RCP8.5
Aglyptodactylus laticeps	Endangered	**0.997***	**1***
Anodonthyla hutchisoni	Endangered	0.152	**0.554**
Anodonthyla montana	Vulnerable	0.203	0.394
Anodonthyla rouxae	Endangered	0.159	0.455
Anodonthyla vallani	Critically endangered	0.497	**0.991***
Boophis andreonei	Vulnerable	0.102	0.153
Boophis axelmeyeri	Vulnerable	0.288	**0.554**
Boophis blommersae	Vulnerable	0.117	0.194
Boophis haematopus	Vulnerable	0.356	0.356
Boophis jaegeri	Vulnerable	0.354	0.361
Boophis sambirano	Vulnerable	0.124	0.177
Boophis tampoka	Endangered	**0.989***	**0.991***
Boophis williamsi	Critically endangered	0.315	**0.659**
Cophyla berara	Critically endangered	**1***	**1***
Gephyromantis ambohitra	Vulnerable	0.101	0.170
Gephyromantis azzurrae	Endangered	**1***	**0.909***
Gephyromantis corvus	Endangered	**0.884**	**1***
Gephyromantis horridus	Endangered	0.168	0.252
Gephyromantis klemmeri	Vulnerable	0.070	0.038
Gephyromantis rivicola	Vulnerable	0.218	**0.700**
Gephyromantis runesweeki	Endangered	-0.002	-0.013

Gephyromantis salegy	Vulnerable	0.135	**0.555**
Gephyromantis schilfi	Vulnerable	-0.018	-0.049
Gephyromantis silvanus	Endangered	0.187	0.173
Gephyromantis striatus	Vulnerable	0.074	0.059
Gephyromantis tandroka	Vulnerable	0.099	0.337
Gephyromantis webbi	Endangered	0.134	0.138
Mantella aurantiaca	Critically endangered	0.336	0.481
Mantella bernhardi	Endangered	**0.932**	**0.989***
Mantella cowanii	Critically endangered	0.198	0.422
Mantella crocea	Endangered	-0.015	-0.036
Mantella expectata	Endangered	**0.784**	**0.829**
Mantella haraldmeieri	Vulnerable	0.368	**0.535**
Mantella madagascariensis	Vulnerable	0.351	0.247
Mantella manery	Vulnerable	0.129	0.030
Mantella milotympanum	Critically endangered	0.012	-0.046
Mantella pulchra	Vulnerable	0.234	**0.587**
Mantella viridis	Endangered	0.285	0.484
Mantidactylus delormei	Vulnerable	-0.017	-0.065
Mantidactylus noralottae	Vulnerable	**0.652**	**0.681**
Mantidactylus pauliani	Critically endangered	0.498	**0.659**
Platypelis alticola	Endangered	0.116	0.3841
Platypelis mavomavo	Endangered	-0.017	-0.034
Platypelis milloti	Endangered	0.438	**0.780**
Platypelis tetra	Endangered	0.217	**0.676**
Platypelis tsaratananaensis	Vulnerable	0.017	0.130
Plethodontohyla brevipes	Endangered	0.026	-0.012
Rhombophryne coronata	Vulnerable	0.344	**0.569**
Rhombophryne coudreaui	Vulnerable	0.318	**0.686**
Rhombophryne guentherpetersi	Endangered	0.129	0.189
Rhombophryne testudo	Vulnerable	0.097	0.455
Scaphiophryne boribory	Endangered	**0.521**	**0.826**
Scaphiophryne gottlebei	Endangered	**1***	**1***

Scaphiophryne menabensis	Vulnerable	**0.961**	**0.992***
Spinomantis brunae	Endangered	0.328	0.477
Spinomantis guibei	Endangered	0.359	**0.510**
Spinomantis microtis	Endangered	0.287	0.401
Stumpffia helenae	Critically endangered	0.487	**0.512**
Stumpffia pygmaea	Vulnerable	0.386	0.367
Tsingymantis antitra	Vulnerable	**0.706**	**0.807**

Chapter 5. Thesis contribution and wider implications

5.1 Overview

This thesis has developed and applied a technique whereby rare species in geographically restricted habitats can be included in spatial Climate Change Vulnerability Assessment (CCVA), through the development of trait distribution models (TDMs). The application of the TDMs to Malagasy amphibians demonstrated that some trait combinations are more vulnerable than others to projected climate change. Arboreal frogs are highly vulnerable even under the business-as-usual RCP (RCP4.5). But the wider implications for the TDM framework suggest potential in assessing climate vulnerability of rare and threatened species in taxa globally. However, a combination of climate change and habitat change reveal a significant impact on Malagasy amphibians; climate-only models for specialised species overpredict current areas of suitability by as much as 60%. Inclusion of habitat variables in TDMs highlights important information and in doing so, TDMs point towards habitat management strategies for communities. TDMs were then put into a planning context, focussing on whether the current system of protected areas offered protection through their areal extent under predicted climate change. CCVA conducted through a TDM framework inclusive of habitat variables, strongly suggests that the areal extent of the PA network in Madagascar offers some protection under climate change. Many future ranges of threatened species fall within PA boundaries but my results indicate that species climate sensitivity is linked to altitudinal zones. Initial concerns for highland species when considering temperature dependent range-shifts, is that any upslope dispersal is constrained by altitudinal limits and therefore, tropical montane species will be highly climate sensitive. However, my results indicated no species loss and little habitat loss because of climate change in highland zones. Therefore, our concern for highland species may be partially misplaced, with lower slopes and lowland regions demonstrating higher levels of climate linked species and habitat loss.

5.2 TDM framework

TDMs are a useable and pragmatic tool which can help to overcome the rare species paradox. TDMs consist of three tables: species traits, species occurrences and environmental variables. TDMs firstly assess traits independently of phylogenetic relationships to produce trait complexes, then pool occurrences of species within a complex to assesses the relationship between a complex and the environment, the latter done with a species distribution model such as MaxEnt (Phillips *et al*., 2006). TDMs are related to RLQ/fourth-corner analysis (Dolédec *et al.*, 1996; Dray and Legendre, 2008; Dray *et al.*, 2014; Duflot *et al.*, 2014) which provides a response of individual traits to the environment, weighted by abundance. Three tables, R (environmental variables), L (species abundance) and Q (trait descriptions for species) form RLQ analysis and combining these tables along an orthogonal axis provides scores for each combination, measuring the link between traits and the environment, one trait at a time. Alternative methods of matching traits to the environment have been used. For example, Generalised Linear Mixed Models (GLMM) have been applied to presence-absence data and produced equivalent results to that of RLQ/Fourth-corner analysis (Jamil *et al.*, 2013), but does not remove the phylogenetic relationship between species and traits. Mechanistic models are considered by some authors as more robust than correlative models and potentially more useful when projecting into future climate conditions (Rowland *et al*., 2011). Whilst mechanistic models may well be available for many ecological questions (Santini *et al.*, 2016), they are data hungry, requiring extensive detail (Kearney and Porter, 2009) from both trait and occurrence data precluding them from practical use in CCVA. TDMs are advantageous in three ways: (a) they remove the phylogenetic link and relate a trait complex to the environment rather than individual traits, (b) they use presence only data and (c) they use software (i.e. MaxEnt) with an accessible graphical user interface allowing results to be mapped out.

The first advantage of TDMs, removal of the phylogenetic link, is important. For many species, quantitative trait data is not available, excluding those species from analysis (Jain *et al.*, 2014). Whilst in theory exclusion can be dealt with by effectively relying on traits exhibited by more common related species (Pollock *et al*., 2012), it is apparent that rare species exhibit idiosyncrasies not found elsewhere within the genus leading to false emphasis on the relative importance of a functional trait. It is highly unlikely that traits have evolved individually as an adaptive response to the environment, rather, specific combinations of traits may have more adaptive value than individual traits considered in isolation (Verberk *et al*., 2013). Therefore, taxonomic groups generally lack the power to detect trait/environment relationships (Mbaka *et al*., 2015) as traits are often correlated to each other (Verberk *et al*., 2013), thus testing the relationship of individual traits to the environment can be misleading (for example, see Angert *et al.*, 2011; Santini *et al.*, 2016). TDMs ordinate trait data to produce a latent variable which describes complexes where species share trait commonalities. When Malagasy amphibians are grouped by K-means clustering, because of trait commonalities, we find that threatened species cluster together. TDMs assume that ecological assembly rules (Keddy, 1992) have acted to produce each complex, the traits exhibited by each complex have coevolved (Verberk *et al*., 2013) and that the behaviour of many can model the system (Levin, 1992).

5.3 Wider application of TDMs

Decision making for conservation is a difficult process, balancing conflicting interests between stakeholders and achieving biodiversity targets. In theory, methods which can highlight a spatial response of species to environmental influences should play an important role in conservation planning, particularly when climate change presents such a significant threat to biodiversity. Yet, inclusion of methods, such as SDMs, which can measure a spatial response to climate are rarely incorporated into decision making for conservation planning (Guisan *et al.*, 2013). Use of modelling is conspicuous by its absence in tropical regions, where most biodiversity is found (Cayuela *et al.*, 2009) but inclusion of modelling as a decision-making tool is hampered by barriers. Uncertainty in different modelling approaches and in projections of future climate (Carvalho *et al.*, 2011; Kujala *et al.*, 2013; see also Chapter 1) both contribute to restricted use of models in conservation planning. But additional restrictions, particularly in tropical regions, inhibit the use of modelling: data availability and expertise. In this section, I will discuss some of the limitations as they affect SDMs and the potential of TDMs to overcome barriers and consequently their wider conservation implications.

5.3.1 Underlying data

The rate of climate change and synergy between other threats, such as habitat loss, creates an immediacy in conducting CCVA for threatened species. Such immediacy in identifying conservation priorities necessitates using the tools and data we have to hand (Mawdsley *et al*., 2009; Rowland *et al*., 2011) rather than waiting for further refinement in both data and models. Such refinement has associated costs, both direct and indirect. Cost can be measured in financial terms as the direct cost of data collection. But also, and more importantly, there are indirect and escalating costs of species and ecosystem loss and the domino effect on the socio-economic stability of societies dependent on surrounding ecosystems (Hannah, 2011). Worryingly, a substantial number of species are too rare to model at 1 km resolution, usually omitting them from CCVA. For example, a study of sub-Saharan amphibian distribution found that 175 out of 191 threatened species lacked enough occurrence data for SDM application at 1° resolution (Platts *et al.*, 2014). In my study, 67% of the 248 Malagasy species considered had insufficient data for applying SDM. What is more, the number of amphibian species in Madagascar has dramatically risen since the beginning of the study in 2014 from 248 to over 300 species when the taxon was reassessed in 2017 (IUCN, 2017). These new species have little in the way of occurrence data associated with them, providing more rationale for the need of TDMs. Given the urgency surrounding many species (Cayuela *et al.*, 2009; Guisan *et al.*, 2013), I initially conceived the TDM framework to use both techniques and data that were widely available, filling the gap for spatial assessment of rare or threatened species where distribution data is sparse.

Data paucity arises for a variety of reasons; extent of the study area, the taxa under study (Cayuela *et al.*, 2009), detectability of species and rarity, to name a few. More common species are regularly recorded as they are more frequently encountered, often near to features such as roads or habitation (Beck *et al.*, 2014). Some species are simply hard to detect because they are cryptic (Frederico *et al.*, 2013), or demonstrate seasonal behavioural changes (Encarnación-Luévano *et al*., 2013), temperature and precipitation changes (Nowakowski *et al.*, 2016), and nocturnal behaviour (Frederico *et al.*, 2013), and therefore also recorded less frequently. Further still, collecting effort fluctuates temporally and regionally; records for Madagascar have decreased over time, whereas Thailand saw a large peak in record collection around the 1990's (Cayuela *et al.*, 2009). Because systematic surveys across large extents for given taxa are rare (Cayuela *et al.*, 2009), TDMs utilise open source and accessible data both in terms of categorising traits and in obtaining occurrence data (e.g. GBIF). Such accessibility reduces costs for conservation assessment both financially and in manpower/time. However, databases such as GBIF are criticised for survey bias and unsubstantiated survey effort (Beck *et al.*, 2014), which reduces faith in results especially when the data are used in the context of SDMs (Oleas *et al.*, 2019). Yet in the framework of conservation assessment, biological databases provide perhaps the only viable option for multiple species over a wide extent, which meets the criteria of being both cost and time effective (Ward *et al.*, 2009).

Methods of spatially accounting for threatened species (filling the data gap) are considered a high priority for CCVA (Foden *et al.*, 2018) and TDMs open up a wide range of taxa, globally, for spatial assessment. The advantage of TDMs is that they pool multiple species to map a trait complex, adding value to rare species (Ferrier and Guisan, 2006). Therefore, common and rare species alike with shared trait attributes contribute to the mapped output and avoid restrictions normally associated with lack of occurrence data for rare species. Single species' spatial responses can then be inferred from their trait complex membership. Whilst inference is not a perfect solution to rare species assessment, it is a step forward from current SDM limitations. An additional benefit of targeting species of conservation concern is that the protection of non-threatened species is often enhanced (Drummond *et al.*, 2010), a role that TDMs can conceivably participate in. But even with such additional techniques in spatial assessment, vital conservation planning cannot be carried out unless it is underpinned with more, and better-quality data (Cayuela *et al.*, 2009). The case of amphibian occurrences in Tanzania, is a prime example. At the beginning of my PhD studies, the initial proposal was to run the study using amphibian species from Madagascar and the Eastern Arc Mountains in Tanzania. Whilst there are good field guides to East African amphibians (Channing and Howell, 2006) and regional experts to provide input (Kim Howell and Michele Menegon, for example), occurrence data for the extent of Tanzania, whether for rare or common species, even within biological databases after records were cleaned, was virtually non-existent (101 useable records). When those data are then restricted to the extent of the Eastern Arc Mountains, spatial modelling of any description was not a viable option, yet in this region there is a desperate need for assessment. There are at least 36 endemic species in the Eastern Arc Mountains, some of which are restricted to single valleys or sites less than 1 km^2 (Menegon and Salvidio, 2005; Rovero and Menegon, 2005; Burgess *et al.*, 2007; Seki *et al.*, 2011a). Of these site-restricted species, at least three (*Nectophrynoides poyntoni* and *N. tornieri* and *Hyperolius kihangensis*) were not seen over a two-year field season (Seki *et al*., 2011b). This concerning absence highlights the need for assessment and, combined with the deficit of database records, that basic advances in how we collect and record biological data (species occurrences) need to be made. Encouraging non-governmental organisations and policy change from government agencies to release biological data under a commons license would boost local records. Furthermore, biological databases would benefit from making simple data improvements, such as requesting that authors verify spatial accuracy of species locations and that databases ensure that records are correctly categorised (Cayuela *et al.*, 2009). For example, in my initial data set from GBIF, at least 2500 records referred to reptile locations despite requesting only Malagasy amphibian records, emphasising that such records need to be carefully evaluated before use (Oleas *et al.*, 2019). Obtaining more occurrences across taxa and large extents is a significant, but necessary challenge; time and budgets are often limited for conservation assessment of regions (Kerr *et al*., 2000), and improved data sharing will surely be a major frontier in enhancing underlying datasets (Rhee 2004; D'Cruze *et al*., 2009). The difficulty will be in encouraging individual researchers to release personal databanks of records for wider conservation use, although initiatives such as iNaturalist (inaturalist.org) do provide a platform for broader data sharing. As does improved synthesis of citizen knowledge through designed participatory surveys (Pédarros et al., 2020). Finally, there is an important caveat; not all records of species occurrences should be released to the wider community. A discussion with Michele Menegon in 2011 revealed that a viper species (*Atheris matildae*) had been newly discovered in the Tanzanian highlands (Menegon *et al*., 2011). Surrounding this exciting discovery were very real concerns that releasing the species location would both help and hinder the species by, respectively, allowing targeted conservation and by inadvertently exposing the species location to collectors.

5.3.2 The role of TDM in conservation

Although distribution modelling demonstrates multiple applications throughout conservation (e.g. CCVA, identifying survey areas, assessing conservation priorities, informing policy; Cayuela *et al.*, 2009), there remains a fundamental issue of the level of expert knowledge required to implement models and translate outputs. Modelling is likely to be omitted from conservation decisions because the variety of methodological options and variability in outputs necessitate expert input, restricting general usability (Guisan *et al.*, 2013). Moreover, omission of modelling can also be attributed to a lack of engagement from both sides of the process, decision makers and scientists alike. Lack of engagement arises due to not understanding each other's needs and consequently, early and necessary consultation (in both directions) in the decision-making process is not undertaken (Addison *et al.*, 2013; Guisan *et al.*, 2013). To overcome this, Addison *et al*. (2013) recommend a 'structured decision-making framework' with 'participatory decision-making' to encourage greater engagement. It is perhaps here, early in the process, that TDMs could be implemented, opening up space for consultation and by doing so, encourage input from land managers and conservation experts alike. TDMs are likely to work in a consultative context; because TDMs pool species, they demonstrate a community-based response to the environment. Such a community centric perspective provides a basis for delivering habitat management strategies and by doing so, encourages participation from a wide range of stakeholders. For taxa which are considered indicators of ecosystem health (Nori *et al.*, 2015), TDMs may also assist in promoting ecosystem services (the mechanism of nature benefiting people). Ecosystem services can be divided into four categories: regulating, provisioning, cultural and supporting services (Millenium Ecosystem Assessment, 2005). TDMs that consider taxa such as amphibians, which have a close link to ecosystem physical structure and functioning (Hocking and Babbitt, 2014), will amongst other things, inform management for supporting services. Furthermore, ecosystem services/community-based strategies to habitat management can potentially shift focus from connecting different habitat patches in the landscape (Tischendorf *et al*., 2003) and move towards the more holistic approach of functional connectivity (Watson *et al.*, 2011). In other words, TDMs identify which components of habitat are important for the community and ecological function of the environment, rather than individual species. For example, amphibians demonstrate ecological redundancy in resources – reliance is on the structure of vegetation to regulate thermal/hydric stasis not in specific plant combinations (Cortés-Gómez *et al*., 2013). Thus, for arboreal amphibians, TDMs suggest that a medium may be struck whereby a managed model is employed to selectively harvest trees, maintaining core habitat structure. The corollary to this is that maintaining leaf litter cover on the forest floor will also encourage persistence of other communities (Whitfield *et al.*, 2007; Edwards *et al.*, 2019). Such a broad brushstroke approach at a scale appropriate for park managers, may make TDMs appealing for PA management and for combining with land-use models, on the condition that local factors are accounted for (Jung *et al.*, 2016). Therefore, TDMs strongly favour participatory stakeholder input at many levels above single species models. But care still needs to be taken with implementing TDMs. The data for TDMs is freely available, as is the software for the SDM portion of the framework; all aspects, notably both MaxEnt and GIS, can now be developed in R (R Core Team, 2018). On one hand, such freedom of access opens up TDMs to multiple users thereby facilitating their use, but TDMs still require a level of expertise to implement, an understanding of the initial problem and the intended purpose of the outputs (Guillera-Arroita *et al.*, 2015).

To solely base conservation action on the output of TDMs or any single model approach would be a mistake due to other challenges in modelling such as, variability between model types, available data and differences in climate scenarios (see Chapter 1). However, one of the challenges of having a nice ability to portray mapped output is that people may believe them uncritically; yet translating the [mapped] results depends very much on the intended application and requires detail on modelled relationships to critically examine maps (Yackulic *et al*., 2013). Translation of mapped output is strongly influenced by variable choice and taxa (Braunisch *et al.*, 2013). For example, range-shift analysis based on temperature dependency inevitably oversimplifies taxa/climate relationships (Rull and Vegas-Vilarrubia, 2006; Raxworthy *et al.*, 2008) and furthermore, drawing conclusions from a broad category of ectotherms (e.g. reptiles and amphibians) fails to reflect substantial eco-physiological differences (Gibbons *et al.*, 2000). A preliminary investigation into upslope shifts exhibited by reptiles and amphibians in Madagascar suggested that range changes of both taxa, are temperature dependent (Raxworthy *et al.*, 2008). However, my data and analysis strongly suggest that inclusion of both precipitation and temperature gradients are required.

The output required by habitat managers will clearly differ to those for CCVA, and likewise from the identification of translocation sites (Guisan *et al.*, 2013). Output is also determined by the nature of the problem a model is applied to. Binary maps (presence/absence) can indicate the overall climate sensitivity of species but for conservation management within the landscape, are not appropriate because they are dependent on the threshold value chosen and say nothing about habitat suitability per grid cell. Further still, binary maps can lead to omission and commission errors in conservation planning because they assume homogenous distributions (Rondinini *et al.*, 2006). Chapter 3 demonstrated that combining climate and habitat variables is crucial for specialist amphibian species and models based on climate-only variables over-predict distributions, by as much as 60% for specialists. For policy makers, such margins of error are simply too much to rely on single models (Sinclair *et al*., 2010; Guisan *et al.*, 2013). Conversely, maps based upon scale of suitability may be misleadingly precise (Sinclair *et al.*, 2010) limiting the role of modelling in conservation planning because of uncertainty in future projections. Whilst solitary TDMs can indicate trends and patterns, the overall danger of using any modelling for conservation planning is that they are used in isolation (Loiselle *et al.*, 2003). TDMs need to be part of the extended family of assessment techniques, joining with multiple SDMs, TBAs, prioritization algorithms (e.g. Zonation) and expert trimming to identify congruence across model platforms thereby reducing uncertainty. As pointed out by Ferrier and Guisan (2006), the challenge is to select the most appropriate approach for the situation at hand. For example, by combining TDMs and TBAs with expert trimming (on TDM mapped outputs), we can refine threatened species prioritization for conservation action. Alternatively, taxon specific, multiple SDMs can be combined with TDMs to identify grid cells which are likely to be subject to rapid change and better target resources/conservation effort. TDMs can then be further used to identify habitat management strategies which maximise biodiversity.

Ecological community (trait) approaches to habitat management, may provide a broad environmental and realistic management strategy, especially in regions where there is extensive anthropogenic pressure on species and habitats (Rogers *et al.*, 2010). Managing forest and vegetation assemblies to the benefit of both the local community and wildlife as climate changes, is a challenge and the potential impact of socio-economic pressure was discussed in Chapters 3 and 4. However, the effectiveness of land management systems will be further altered by edge effects, where the environmental characteristics of the matrix surrounding fragmented habitat differ considerably (Stevens and Husband, 1998), influencing microclimate changes from the interface of the edge through to the interior of fragments. Fragmentation of habitat and connected impacts on wildlife is an expanding frontier of research and feasibly one which trait-led research (TDMs) could bring an alternative perspective to. For example, amphibians actively avoid dry, exposed edges of forest fragments (Lehtinen *et al*., 2003). But whether species are susceptible to edge effects is dependent on functional traits; some functional traits are more vulnerable than others to changes in temperature (Scheffers *et al.*, 2013; Watling and Braga, 2015) and the integrity of the landscape (Summers *et al.*, 2012). As a result, species of amphibian in Madagascar have been shown to survive in fragmented forest environments, if sufficient microhabitat remains, but the proportion of functional traits changes with habitat fragment size (Vallan, 2000; Riemann *et al.*, 2017). The impact of edge effects on functional connectivity through TDMs will be an insightful measure of conservation action.

5.4 Future research directions

There is absolutely no doubt that species response to climate change is complex. Simple range shift theories centred on temperature dependency suggest an upslope movement for many species (Peters and Darling, 1985; Bentley *et al*., 2018), which has concerning implications for those species at the top of the hill. Chapter 2 clearly demonstrated an upslope shift of species within a trait complex, in response to temperature and precipitation changes by the end of the century. Most species accumulated around the mid-altitudinal area and coincided with a shift into zones with high topographic heterogeneity, which perhaps hints at the presence of topographic refugia (Dobrowski, 2011). Chapter 4 showed that no threatened tropical montane species are predicted to go extinct due to climate-led changes. However, modelling rarely accounts for anthropogenic/socio-economic impacts and is dominated by biological criteria (Rogers *et al.*, 2010). Changes in patterns of agriculture incited by climate shifts (Bush, 2002) may yet cause losses of species in montane habitats. Inclusion of land-use measures into TDMs is problematic, partially due to the complexity of the human-landscape relationship (Carpenter *et al.*, 2006; Rogers *et al.*, 2010) and partially because in order to provide long-term projections, the land-use model implemented really needs to be dynamic (Ficetola *et al.*, 2010). A dynamic land-use model is desirable because land-use is driven by a range of socio-economic factors, which in turn are propelled by environmental cues such as climate (Falcucci *et al*., 2006). Combining the framework of Rogers *et al*. (2010) with TDMs may lead to additional revelations of community responses to the environment, improving conservation planning responses further. Conservation priorities across Madagascar have been previously identified by using multiple modelling tools across taxa, where rare species were included as point occurrences only (Kremen *et al.*, 2008), but aspects of communities and anthropogenic use of the landscape were absent. It would therefore be interesting to repeat such a study using TDMs to fulfil the rare species deficit across multiple taxa, and further expand the study to include aspects of community ecology and land-use.

Although distribution models may be dominated by biological criteria, they have so far omitted mechanisms of species interaction (HilleRisLambers *et al.*, 2013; Schleuning *et al.*, 2020). For montane species, such omission may have critical implications on species survival, due to increasing elevational range shifts from those species lower down the slopes. But accounting for biotic interaction in the modelling environment is simply difficult, whether in SDMs or TDMs. Species do not work in isolation and are instead subject to community based biotic interactions, notably interspecific competition which has shaped community structure in the past (Lavergne *et al.*, 2010; HilleRisLambers *et al.*, 2013). Competitors, mutualists, facilitators and consumers all play a role in influencing a species performance particularly at range limits (Faisal *et al.*, 2010; HilleRisLambers *et al.*, 2013), and modifying a species response across its range (Lavergne *et al.*, 2010) sometimes in unexpected ways (HilleRisLambers *et al.*, 2013). Both TDMs and SDMs assume that species interactions remain temporally static but, such an assumption is highly unlikely, with communities and species living in a state of dynamic flux (Ferrier and Guisan, 2006). Therefore, a measure of trait interaction (community dynamics) may provide a more useful measure of community response under climate scenarios (McMahon *et al.*, 2011) and be applicable in helping to determine trailing and leading edges of distribution (see Anderson *et al*., 2009). TDMs, as community models, grant a possible technique to measure biotic interaction between communities and a recent study suggests that such measures will crucially improve assessments of interacting species (Schleuning *et al*., 2020). Biotic interaction between TDM communities could be measured by Spatial Network Analysis or a Spatial Ecological Network (SEN), where the importance of spatial location and network position is characterised for each actor (in this case, community), a technique which has been used to assess disease outbreaks (Firestone *et al.*, 2011; Marquetoux *et al.*, 2016) and has potential in conservation planning (Gonzalez *et al*., 2017). Alternatively, through a weighted link between communities per grid cell, a measure of the strength of interaction between traits across environmental gradients could be applied. Furthermore, there would be great benefit linking emerging pathogens, such as the fungus *Batrachochytrium dendrobatidis* (Bd) (Lips *et al.*, 2006) associated with mass amphibian declines (Stuart *et al.*, 2004; Lips *et al.*, 2006), to community dynamics and distributional data, particularly in regions where the disease is novel (Bletz *et al.*, 2015). TDMs are well suited to measuring the impact of Bd as species traits and specialisation appear to play a role in susceptibility to the disease; species losses from Bd in central America are greatest in cool, moist, high elevation sites (Puschendorf *et al.*, 2011) and for stream-breeding frogs (La Marca *et al.*, 2005). Additionally, pristine environments may increase extinction risk from Bd (Becker and Zamudio, 2011) placing further extinction pressure on habitat specialists. Moreover, some frog species may act as vectors for the fungus, of which several arboreal species have been implicated (Lips *et al.*, 2006, Hudson, 2016) through arboreal disease reservoirs (Cossel and Lindquist, 2009, Hudson, 2016).

Apart from integrating multiple techniques (Spatial Network Analysis and TDMs), the challenge for further analysis of community dynamics or disease networks is the improvement of survey data. Improving survey data may take two forms by i) targeting areas to survey to save time and effort and conserve valuable resources and ii) improving techniques used in collecting data in the field. TDMs may directly improve survey data, as a tool for targeted surveys. SDMs and occupancy models have already been used to guide and inform survey efforts to good effect (Peterman *et al*., 2012, Webb *et al*., 2014). TDMs can highlight grid cells of rapid change for communities, thereby allowing researchers to select areas which would benefit from detailed monitoring. Alternatively, TDMs combined with SDMs may also highlight areas of greatest uncertainty in climate change projections, again allowing targeted surveys. When specific locations are identified, monitoring techniques need to be employed that are suitable for the challenges of that location and duration of study.

The specific challenges for monitoring of amphibians in the field, are that the census techniques employed are often time consuming, need to be targeted towards different life histories (Doan, 2003; Dodd, 2010), account for seasonal changes, vary in efficacy between different habitat types and that some species are cryptic; all of which are a major hurdle for analysis of amphibian data (Dodd, 2010; Ficetola, 2015). Typically, multiple census techniques are employed to capture the amphibian diversity within a site (Dodd, 2010; Rosa *et al.*, 2012). For amphibians, acoustic monitoring using automated recording systems offers a good long-term approach to extended field studies especially when cryptic species are of interest or manpower is restricted (Aide *et al.*, 2013). Nevertheless, the estimation of population size or density from acoustic surveys is difficult, particularly from automated recording systems. A sound recorder with two or more microphones can be configured as an interferometer (Parsons *et al.*, 2009), and it is possible to determine the angle to the source of the call from the difference in signal phase recorded at the interferometer. It is therefore conceivable to distinguish individuals by their location. Although conceptually simple, in practice interferometry with animal calls can be challenging because the calls are modulated in amplitude and frequency. Whilst automated recording systems have a long history within amphibian monitoring and species detection (Aide *et al.*, 2013; Marques *et al.*, 2013), there have been no studies which explicitly use fixed dual microphone arrays to provide estimates of amphibian abundance. Abundance and presence data from automated recording systems will offer improvements to community TDMs for amphibian species. The use of TDMs in epizootic research will present further challenges in data collection. Monitoring the spread of Bd across a landscape requires rapid identification of the disease presence, but until recently, identification was restricted by laboratory constraints (Dillon *et al.*, 2017). New lateral-flow assay techniques in fungal pathogen identification are simple, fast, potentially cheap and above all, portable, front-line detection method for Bd in the field (Dillon *et al.*, 2017).

TDMs for Malagasy amphibians warn of large contractions to trait complex ranges and of losses of threatened species. The initial models (Chapter 2) were built using Worldclim variables (Hijmans *et al*. 2005), but I strongly suspect that new variables such as solar radiation, wind speed and water vapor pressure available from Worldclim2 (Fick and Hijmans, 2017), would further influence ranges of traits for amphibians. Solar radiation certainly affects egg and tadpole development (Middleton *et al.*, 2001), whilst wind speed and water vapor pressure will both strongly effect hydric stasis in amphibians (Tracy, 1976; Wygoda, 1988). Desiccation proneness has been demonstrated to be a key trait in determining amphibian distributions throughout forest patches (Watling and Braga, 2015), a trait that I expect to be more acutely demonstrated through the ranges of arboreal species than other complexes due to their potentially increased exposure to such variables (see Wygoda, 1988). But exactly how these variables would impact trait distributions would be an extremely interesting area for future research.

5.5 Conclusions

Trait-based ecology held an elusive promise of connecting niche-based systems to community patterns and only in recent years, with new statistical tools, has begun to realise on the promise (Cadotte *et al.*, 2015). TDMs do not account for abundances due to their pragmatic nature – they are designed to incorporate rare species and avoid data constraints – and that is an area for progression. But, TDMs have combined multiple traits and provided trait-based ecological research a platform to consider responses away from individual assembly mechanisms, thereby advancing the field of research. In addition, the potential application of TDMs in both inclusion of biotic interaction and epidemiology is an exciting frontier for research. Overall, TDMs have been effective in conducting CCVA for threatened species in tropical montane systems in Madagascar, although they have identified that these regions are not necessarily the conservation priority first assumed. Instead, it appears that conservation effort is equally as needed to maintain the remaining habitat in mid-altitudinal zones, the formation of upslope connectivity pathways from lowland zones and conservation of arboreal obligates. It will be interesting to apply TDMs to amphibians in other geographic localities, especially mountainous regions in East Africa with numerous strict endemic amphibians (Seki *et al*., 2011b), and to other taxa. The growing demand to comprehensively included CCVA in Red List assessments and conservation planning (Foden *et al.*, 2013; Foden and Young, 2016; IUCN SSC Standards and Petitions Subcommittee, 2017) demonstrates a substantial need for TDMs, to avoid previous assessment hurdles of data scarcity and small distribution ranges.

Yet the contribution to protecting nature goes beyond CCVA. The interconnectivity of the natural world is fundamentally intertwined with human development, health, well-being, culture and productivity. The influence of biodiversity on society can be either nebulous or tangible, but the loss of biodiversity, which is being fuelled by human activities, is self-harming; climate change for example, is in part caused by the loss of biodiversity (Lovejoy, 2019). Various global platforms exist which promote the critical objective of sustainable practices to preserve biodiversity, such as: UN Sustainable Development Goals (SDGs), strategic goals of Aichi Biodiversity Targets, and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). Models which convey details of ecosystem services can inform sustainable development and, in this area, TDMs offer the potential to make a truly exciting and significant contribution to global conservation. If the legacy from this research were the contribution of TDMs to sustainable development, making a genuine and lasting impact on conserving biodiversity, then that is an outcome that I would be more than happy with.

5.6 References

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6. Appendices

Appendix I. Abstracts: Co-authored papers.

I present here abstracts of journal articles and other research to which I contributed during my PhD studies. Articles have relevance to the amphibian conservation aspect of my PhD.

Articles are presented in reverse chronological order and have contributed to this thesis from their findings. For example, the contributed thesis chapter '*Daily activity profiles of the golden mantella (Mantella aurantiaca) under different temperature regimes*' demonstrated that both available water (relative humidity) and temperature were important determinants of species exposure to the environment and helped to reinforce ideas behind species exposure expressed in Chapters 2 and 3. Furthermore, the importance of leaf-litter in mitigating against climate change (research article; *Microhabitat preference of the critically endangered golden mantella frog in Madagascar*) was discussed in Chapter 3. Under predicted climate change, golden mantellas (*Mantella aurantiaca*) are projected to demonstrate a 93% reduction in range size by 2085, providing species specific results that support my own findings. Within this thesis, Golden mantellas belong to complex of habitat specialists (complex E), which is projected to undergo a 98% reduction in range size (RCP8.5, 2085). The article by Dillon *et al*. (2017) was used in this thesis to support possible avenues of future research for TDMs in epidemiology through coupling TDMs with a rapid qualitative assay developed by the authors. The article by Tapley *et al*. (2015) was used throughout the thesis, particularly in connection with ex-situ strategies for conservation of arboreal amphibians, whilst Bungard *et al*. (2014) supported arguments relating to arboreal amphibian habitat use.

Contribution to PhD thesis chapter – Chapter 3. Daily activity profiles of the golden mantella (*Mantella aurantiaca*) under different temperature regimes.

In Edwards, W. M. (2019) 'Conservation of the golden mantella in Madagascar: Integrating in situ and ex situ research.' PhD thesis, University of Kent.

Wayne M. Edwards, Richard A. Griffiths and **Michael J. Bungard**.

Abstract - The critically endangered golden mantella (*Mantella aurantiaca*) is an iconic, montane, endemic frog found in the Moramanga district, Madagascar. Ecological and behavioural data for this highly threatened species are sparse, and much of the future mitigation and habitat protection work will need to be based upon scientific evidence provided by both in situ and ex situ studies focused on habitat preferences and requirements. Rare species with cryptic lifestyles are almost impossible to study in the wild, especially if continuous behavioural data over prolonged periods are required. This study therefore utilized environmental information gathered in the field to design a system where these can be measured in captivity. Using climatically controlled chambers (the "Froggotrons"), we analysed the 24-hour activity budget of the golden mantella and how different temperatures impact on their daily activity profile. Golden mantellas showed a bimodal pattern of activity during the day with much less activity during the night. Frogs kept at warmer temperatures (20 - 25°C) were more active than those kept under cooler conditions (16 - 19°C). However, the bimodal pattern was retained under the different temperatures, so there was no temperature-induced phase shift. Most activity was observed when humidity levels were above 85%. These findings can inform ongoing field surveys through determining the optimum times of day to either capture or count golden mantellas for further conservation actions.

Contribution to PhD thesis chapter – Chapter 5. Predicted impact of climate change on the distribution of the Critically Endangered golden mantella (Mantella aurantiaca) in Madagascar.

In Edwards, W. M. (2019) 'Conservation of the golden mantella in Madagascar: Integrating in situ and ex situ research.' PhD thesis, University of Kent.

Wayne M. Edwards, **Michael J. Bungard** and Richard A. Griffiths

Abstract - The impact of climate change on Malagasy amphibians remains poorly understood. Equally, deforestation, fragmentation and lack of connectivity between forest patches may leave vulnerable species isolated in habitat that no longer suits their environmental or biological requirements. We assess the predicted impact of climate change by 2085 on the potential distribution of a Critically Endangered frog species, the golden mantella (*Mantella aurantiaca*), that is confined to a small area of the central rainforest of Madagascar. We identify potential population distributions and climatically stable areas. Results suggest a potential south-eastwardly shift away from the current range and a decrease in suitable habitat from 2110 km^2 under current climate to between 112 km^2 – 138 km^2 by the year 2085 – less than 7% of currently available suitable habitat. Results also indicate that the amount of golden mantella habitat falling within protected areas decreases by 86% over the same period. We recommend research to ascertain future viability and the feasibility of expanding protection to newly identified potential sites. This information can then be considered in future conservation actions such as habitat restoration, translocations, re-introductions or the siting of further wildlife corridors or protected areas.

Research article — Microhabitat preference of the critically endangered golden mantella frog in Madagascar.

Herpetological Journal (2019)

Volume 29 (October), Pages 207–213, doi: 10.33256/hj29.4.207213.

Wayne M. Edwards, Richard A. Griffiths, **Michael J. Bungard**, Eddie F. Rakotondrasoa, Julie H. Razafi manahaka, Pierre Razafindraibe, Raphali R. Andriantsimanarilafy, and Joseph C. Randrianantoandro.

Abstract — The golden mantella (*Mantella aurantiaca*) is a critically endangered (CR) frog, endemic to the eastern rainforests of Madagascar. Although the species is very popular in the pet trade and widely bred in captivity, its specific habitat requirements in the wild are poorly understood. Ten forested sites in the Moramanga district of Madagascar were surveyed for microhabitat and environmental variables, and the presence or absence of golden mantellas in quadrats positioned along transects in the vicinity of breeding sites. Mixed models were used to determine which variables best explained microhabitat use by golden mantellas. Sites where golden mantellas were found tended to have surface temperatures of 20-23 ˚C, UVB levels of about 2.9 µW/cm2, about 30% canopy cover, and around 30% herbaceous cover. Within sites, golden mantellas preferred microhabitats that had 70% leaf litter coverage and relatively low numbers of tree roots. This information can be used to improve the identification and management of habitats in the wild, as well as to refine captive husbandry needs.

Research article — Tracking the Amphibian Pathogens *Batrachochytrium Dendrobatidis* and *Batrachochytrium Salamandrivorans* Using a Highly Specific Monoclonal Antibody and Lateral-Flow Technology.

Microbial Biotechnology (2017)

Volume 10 (2), Pages 381–394. doi: 10.1111/1751-7915.12464.

Michael J. Dillon, Andrew E. Bowkett, **Michael J. Bungard**, Katie M. Beckman, Michelle F. O'Brien, Kieran Bates, Matthew C. Fisher, Jamie R. Stevens, and Christopher R. Thornton.

Abstract — The fungus *Batrachochytrium dendrobatidis* (Bd) causes chytridiomycosis, a lethal epizootic disease of amphibians. Rapid identification of the pathogen and biosecurity is essential to prevent its spread, but current laboratory-based tests are time-consuming and require specialist equipment. Here, we describe the generation of an IgM monoclonal antibody (mAb), 5C4, specific to Bd as well as the related salamander and newt pathogen *Batrachochytrium salamandrivorans* (Bsal). The mAb, which binds to a glycoprotein antigen present on the surface of zoospores, sporangia and zoosporangia, was used to develop a lateral-flow assay (LFA) for rapid (15 min) detection of the pathogens. The LFA detects known lineages of Bd and also Bsal, as well as the closely related fungus *Homolaphlyctis polyrhiza*, but does not detect a wide range of related and unrelated fungi and oomycetes likely to be present in amphibian habitats. When combined with a simple swabbing procedure, the LFA was 100% accurate in detecting the water-soluble 5C4 antigen present in skin, foot and pelvic samples from frogs, newts and salamanders naturally infected with Bd or Bsal. Our results demonstrate the potential of the portable LFA as a rapid qualitative assay for tracking these amphibian pathogens and as an adjunct test to nucleic acid-based detection methods.

Research article — Amphibians and Conservation Breeding Programmes: Do All Threatened Amphibians Belong on the Ark?

Biodiversity and Conservation (2015)

Volume 24, Pages 2625 – 2646, doi: 10.1007/s10531-015-0966-9.

Benjamin Tapley, Kay S. Bradfield, Christopher Michaels, and **Mike Bungard**.

Abstract — Amphibians are facing an extinction crisis, and conservation breeding programmes are a tool used to prevent imminent species extinctions. Compared to mammals and birds, amphibians are considered ideal candidates for these programmes due to their small body size and low space requirements, high fecundity, applicability of reproductive technologies, short generation time, lack of parental care, hard wired behaviour, low maintenance requirements, relative cost effectiveness of such programmes, the success of several amphibian conservation breeding programmes and because captive husbandry capacity exists. Superficially, these reasons appear sound and conservation breeding has improved the conservation status of several amphibian species, however it is impossible to make generalisations about the biology or geo-political context of an entire class. Many threatened amphibian species fail to meet criteria that are commonly cited as reasons why amphibians are suitable for conservation breeding programmes. There are also limitations associated with maintaining populations of amphibians in the zoo and private sectors, and these could potentially undermine the success of conservation breeding programmes and reintroductions. We recommend that species that have been assessed as high priorities for ex situ conservation action are subsequently individually reassessed to determine their suitability for inclusion in conservation breeding programmes. The limitations and risks of maintaining ex situ populations of amphibians need to be considered from the outset and, where possible, mitigated. This should improve programme success rates and ensure that the limited funds dedicated to ex situ amphibian conservation are allocated to projects which have the greatest chance of success.

Research article — The habitat use of two species of Day Geckos (*Phelsuma ornata* and *Phelsuma guimbeaui*) and implications for conservation management in island ecosystems.

Herpetological Conservation and Biology (2014)

Volume 9 (2), Pages 551−562.

Michael John Bungard, Carl Jones, Vikash Tatayah and Diana J. Bell.

Abstract — Many fragile ecosystems across the globe are islands with high numbers of endemic species. Most tropical islands have been subject to significant landscape alteration since human colonisation, with a consequent loss of both habitat and those specialist species unable to adapt or disperse in the face of rapid change. Day geckos (genus *Phelsuma*) are thought to be keystone species in their habitats and are, in part, responsible for pollination of several endangered endemic plant species. However, little is known about key drivers of habitat use which may have conservation implications for the genus. We assessed the habitat use of two species of *Phelsuma* (*Phelsuma ornata* and *Phelsuma guimbeaui*) in Mauritius. Both species showed a strong affinity with tree trunks, specific tree architecture and are both restricted to native forest. Tree hollows or cavities are also important for both species and are a rarely documented microhabitat for arboreal reptiles. Both *P. ornata* and *P. guimbeaui* avoid areas of high disturbance. Our data suggest that active conservation of *Phelsuma* requires not only the protection and restoration of native forest, but also implementation of forestry practices designed to ensure the presence of suitable trees.

Appendix II. Species considered in analysis

Table 1. Species considered in analysis and their IUCN Red List status in 2014.

Species	**IUCN status**
Aglyptodactylus laticeps	Endangered
Aglyptodactylus madagascariensis	Least concern
Aglyptodactylus securifer	Least concern
Anodonthyla boulengeri	Least concern
Anodonthyla hutchisoni	Endangered
Anodonthyla jeanbai	Data deficient
Anodonthyla montana	Vulnerable
Anodonthyla moramora	Data deficient
Anodonthyla nigrigularis	Data deficient
Anodonthyla pollicaris	Data deficient
Anodonthyla rouxae	Endangered
Anodonthyla theoi	Data deficient
Anodonthyla vallani	Critically endangered
Blommersia blommersae	Least concern
Blommersia domerguei	Least concern
Blommersia grandisonae	Least concern
Blommersia kely	Least concern
Blommersia sarotra	Data deficient
Blommersia wittei	Least concern
Boehmantis microtympanum	Endangered
Boophis albilabris	Least concern
Boophis albipunctatus	Least concern
Boophis andohahela	Data deficient
Boophis andreonei	Vulnerable
Boophis anjanaharibeensis	Data deficient
Boophis ankaratra	Least concern
Boophis axelmeyeri	Vulnerable

Boophis blommersae	Vulnerable
Boophis boehmei	Least concern
Boophis bottae	Least concern
Boophis brachychir	Data deficient
Boophis burgeri	Data deficient
Boophis doulioti	Least concern
Boophis elenae	Data deficient
Boophis englaenderi	Data deficient
Boophis erythrodactylus	Least concern
Boophis feonnyala	Data deficient
Boophis goudoti	Least concern
Boophis guibei	Least concern
Boophis haematopus	Vulnerable
Boophis hillenii	Data deficient
Boophis idae	Least concern
Boophis jaegeri	Vulnerable
Boophis laurenti	Data deficient
Boophis liami	Data deficient
Boophis lichenoides	Least concern
Boophis lilianae	Data deficient
Boophis luteus	Least concern
Boophis madagascariensis	Least concern
Boophis majori	Near threatened
Boophis mandraka	Data deficient
Boophis marojezensis	Least concern
Boophis microtympanum	Least concern
Boophis miniatus	Least concern
Boophis occidentalis	Near threatened
Boophis opisthodon	Least concern
Boophis pauliani	Least concern
Boophis periegetes	Data deficient
Boophis picturatus	Least concern

Boophis pyrrhus	Least concern
Boophis rappiodes	Least concern
Boophis reticulatus	Least concern
Boophis rhodoscelis	Near threatened
Boophis rufioculis	Near threatened
Boophis sambirano	Vulnerable
Boophis schuboeae	Data deficient
Boophis septentrionalis	Data deficient
Boophis sibilans	Data deficient
Boophis solomaso	Data deficient
Boophis tampoka	Endangered
Boophis tasymena	Least concern
Boophis tephraeomystax	Least concern
Boophis viridis	Least concern
Boophis vittatus	Least concern
Boophis williamsi	Critically endangered
Boophis xerophilus	Data deficient
Cophyla berara	Critically endangered
Cophyla occultans	Data deficient
Cophyla phyllodactyla	Least concern
Dyscophus antongilii	Near threatened
Dyscophus guineti	Least concern
Dyscophus insularis	Least concern
Gephyromantis ambohitra	Vulnerable
Gephyromantis asper	Least concern
Gephyromantis azzurrae	Endangered
Gephyromantis blanci	Near threatened
Gephyromantis boulengeri	Least concern
Gephyromantis cornutus	Data deficient
Gephyromantis corvus	Endangered
Gephyromantis decaryi	Near threatened
Gephyromantis eiselti	Data deficient

Gephyromantis enki	Data deficient
Gephyromantis granulatus	Least concern
Gephyromantis horridus	Endangered
Gephyromantis klemmeri	Vulnerable
Gephyromantis leucocephalus	Near threatened
Gephyromantis leucomaculatus	Near threatened
Gephyromantis luteus	Least concern
Gephyromantis malagasius	Least concern
Gephyromantis moseri	Least concern
Gephyromantis plicifer	Near threatened
Gephyromantis pseudoasper	Least concern
Gephyromantis redimitus	Least concern
Gephyromantis rivicola	Vulnerable
Gephyromantis runewsweeki	Endangered
Gephyromantis salegy	Vulnerable
Gephyromantis schilfi	Vulnerable
Gephyromantis sculpturatus	Least concern
Gephyromantis silvanus	Endangered
Gephyromantis spiniferus	Near threatened
Gephyromantis striatus	Vulnerable
Gephyromantis tandroka	Vulnerable
Gephyromantis thelenae	Data deficient
Gephyromantis tschenki	Data deficient
Gephyromantis ventrimaculatus	Least concern
Gephyromantis webbi	Endangered
Gephyromantis zavona	Data deficient
Guibemantis albolineatus	Data deficient
Guibemantis bicalcaratus	Least concern
Guibemantis depressiceps	Least concern
Guibemantis flavobrunneus	Least concern
Guibemantis kathrinae	Data deficient
Guibemantis liber	Least concern

Guibemantis pulcher	Least concern
Guibemantis punctatus	Data deficient
Guibemantis timidus	Least concern
Guibemantis tornieri	Least concern
Heterixalus alboguttatus	Least concern
Heterixalus andrakata	Least concern
Heterixalus betsileo	Least concern
Heterixalus boettgeri	Least concern
Heterixalus carbonei	Near threatened
Heterixalus luteostriatus	Least concern
Heterixalus madagascariensis	Least concern
Heterixalus punctatus	Least concern
Heterixalus rutenbergi	Near threatened
Heterixalus tricolor	Least concern
Heterixalus variabilis	Least concern
Hoplobatrachus tigerinus	Least concern
Laliostoma labrosum	Least concern
Madecassophryne truebae	Endangered
Mantella aurantiaca	Critically endangered
Mantella baroni	Least concern
Mantella bernhardi	Endangered
Mantella betsileo	Least concern
Mantella cowanii	Critically endangered
Mantella crocea	Endangered
Mantella ebenaui	Least concern
Mantella expectata	Endangered
Mantella haraldmeieri	Vulnerable
Mantella laevigata	Near threatened
Mantella madagascariensis	Vulnerable
Mantella manery	Vulnerable
Mantella milotympanum	Critically endangered
Mantella nigricans	Least concern

Mantella pulchra	Vulnerable
Mantella viridis	Endangered
Mantidactylus aerumnalis	Least concern
Mantidactylus albofrenatus	Data deficient
Mantidactylus alutus	Least concern
Mantidactylus ambohimitombi	Data deficient
Mantidactylus ambreensis	Least concern
Mantidactylus argenteus	Least concern
Mantidactylus bellyi	Least concern
Mantidactylus betsileanus	Least concern
Mantidactylus biporus	Least concern
Mantidactylus bourgati	Data deficient
Mantidactylus brevipalmatus	Least concern
Mantidactylus charlotteae	Least concern
Mantidactylus cowanii	Near threatened
Mantidactylus curtus	Least concern
Mantidactylus delormei	Vulnerable
Mantidactylus femoralis	Least concern
Mantidactylus grandidieri	Least concern
Mantidactylus guttulatus	Least concern
Mantidactylus lugubris	Least concern
Mantidactylus madecassus	Endangered
Mantidactylus majori	Least concern
Mantidactylus melanopleura	Least concern
Mantidactylus mocquardi	Least concern
Mantidactylus noralottae	Vulnerable
Mantidactylus opiparis	Least concern
Mantidactylus pauliani	Critically endangered
Mantidactylus tricinctus	Data deficient
Mantidactylus ulcerosus	Least concern
Mantidactylus zipperi	Least concern
Mantidactylus zolitschka	Data deficient

Paradoxophyla palmata	Least concern
Paradoxophyla tiarano	Data deficient
Platypelis alticola	Endangered
Platypelis barbouri	Least concern
Platypelis cowani	Data deficient
Platypelis grandis	Least concern
Platypelis mavomavo	Endangered
Platypelis milloti	Endangered
Platypelis pollicaris	Data deficient
Platypelis tetra	Endangered
Platypelis tsaratananaensis	Vulnerable
Platypelis tuberifera	Least concern
Plethodontohyla angulifera	Data deficient
Plethodontohyla bipunctata	Least concern
Plethodontohyla brevipes	Endangered
Plethodontohyla fonetana	Endangered
Plethodontohyla guentheri	Data deficient
Plethodontohyla inguinalis	Least concern
Plethodontohyla mihanika	Least concern
Plethodontohyla notosticta	Least concern
Plethodontohyla ocellata	Least concern
Plethodontohyla tuberata	Vulnerable
Ptychadena mascareniensis	Least concern
Rhombophryne alluaudi	Least concern
Rhombophryne coronata	Vulnerable
Rhombophryne coudreaui	Vulnerable
Rhombophryne guentherpetersi	Endangered
Rhombophryne laevipes	Least concern
Rhombophryne minuta	Data deficient
Rhombophryne serratopalpebrosa	Vulnerable
Rhombophryne testudo	Vulnerable
Scaphiophryne boribory	Endangered

Scaphiophryne brevis	Least concern
Scaphiophryne calcarata	Least concern
Scaphiophryne gottlebei	Endangered
Scaphiophryne madagascariensis	Near threatened
Scaphiophryne marmorata	Vulnerable
Scaphiophryne menabensis	Vulnerable
Scaphiophryne obscura	Data deficient
Scaphiophryne spinosa	Least concern
Scaphiophryne verrucosa	Data deficient
Spinomantis aglavei	Least concern
Spinomantis bertini	Near threatened
Spinomantis brunae	Endangered
Spinomantis elegans	Vulnerable
Spinomantis fimbriatus	Least concern
Spinomantis guibei	Endangered
Spinomantis massi	Vulnerable
Spinomantis microtis	Endangered
Spinomantis peraccae	Least concern
Spinomantis phantasticus	Least concern
Stumpffia gimmeli	Least concern
Stumpffia grandis	Data deficient
Stumpffia helenae	Critically endangered
Stumpffia psologlossa	Data deficient
Stumpffia pygmaea	Vulnerable
Stumpffia roseifemoralis	Data deficient
Stumpffia tetradactyla	Data deficient
Stumpffia tridactyla	Data deficient
Tsingymantis antitra	Vulnerable
Wakea madinika	Data deficient

7. Abbreviations

Abbreviation	Meaning
ACSAM	A Conservation Strategy for the Amphibians of Madagascar
AIC_c	Akaike Information Criteria
AUC	Area Under the Curve
Bd	*Batrachochytrium dendrobatidis*
cAIC	Conditional Akaike Information Criteria
CATPCA	Categorical principal components analysis
CCS	Climate Change Integrated Conservation Strategies
CCVA	Climate Change Vulnerability Assessment
DEM	Digital elevation model
EVI	Enhanced vegetation index
GAM	General additive model
GAMM	Generalised additive mixed model
GCM	General circulation model
GIS	Geographic information systems
GLMM	Generalised linear mixed model
IPCC-AR5	Intergovernmental Panel on Climate Change’s Fifth Assessment Report
IUCN	International Union for the Conservation of Nature
MCP	Minimum convex polygon
PA	Protected area
PET	Potential evapotranspiration
RCM	Regional climate models
RCP	Representative Concentration Pathway
ROC	Receiver Operating Characteristic
SDM	Species Distribution Model
svl	Snout-vent-length
TBA	Trait Based Assessment
TDM	Trait Distribution Model
TSS	True Skills Statistic
WD	Water deficit