The importance of biotic interactions and climate change on avifaunal range limits of the Albertine rift

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Abstract

Understanding species distribution ecology is essential given the growing need to understand how species will react to climate change and invasion. Understanding the processes by which distribution limits are set is necessary to build accurate distribution models, yet the role of biotic interactions (e.g. competition, predation, disease, parasitism) in determining range limits is uncertain, despite evidence that incorporating biotic information improves the accuracy of these models.

By examining the elevational variability of Afromontane, avian range limits across several communities, we add to reports indicating that environmental conditions are generally more important in determining both high and low stress range limits across an environmental gradient. However, we note that biotic interactions may still be more important at low stress limits than they are at high stress limits and that the processes that limit ranges appear to be different at low and high stress limits. High stress range limits appeared to be much more variable, stimulating new and unexpected questions.

We go on to document how distribution limits of avifauna have shifted in two Ugandan national parks. We tentatively conclude that range shifts may have occurred over the last decade, at a rate faster than one would have expected species to move merely based on the warming that has occurred. This indicated that warming may not be the only factor that is causing species' upper limits to shift upwards in elevation.

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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.

For Laurian, U.W.A. Park Ranger – a life saver

Chapter 1: Introduction

The study of range limits concerns identifying the trends and mechanisms that govern where populations are able to colonise and survive. No species occurs ubiquitously, and investigations into why species might be unable to expand their distributions without hindrance have stimulated evolutionary and biogeographic discourse ever since the works of Darwin (1859), with the discussion focussed more recently by MacArthur (1972). As time has progressed, our ability to verify theories related to distributions has increased as an extensive literature of studies adds to our understanding of the topic. Developments in the field have often arisen from improved understanding of the biological processes that generate limits, including behaviour (Jankowski et al. 2010), particularly movement patterns (Darling et al. 2008), genetics (Sanford et al. 2006), and species interactions (Gross and Price 2000); producing an extensive body of theory to understand the mechanics of range limits. Ultimately, the explanation of why a species exists in one place but not another must relate to fundamental life traits, such as the fecundity, mortality, immigration, and emigration rates of the population (Gaston 2009). Abiotic factors affect how these biological traits resolve to generate range limits. Identifying the relative importance of abiotic and biotic factors in determining range limits has been a key area of research (Sexton et al. 2009, Cahill et al. 2014). As recent species distribution shifts driven by climate change and species introductions have disrupted communities and their functions (Mack et al. 2000), an understanding of how limits will continue to change is an ecological priority. Newfound knowledge on the topic has been applied to species distribution modelling with a view to predicting how species will react to changes in their environment (Hijmans and Graham 2006) and used to better predict how invasions will occur (Nunez and Medley 2011). Given the appreciation of the risks posed to natural systems by climate change and species movement (Williams et al. 2003), including the risk presented from species invasions and range shifts, the benefits to be gained from improving the predictive capability of distribution models are apparent.

In classical models of species distributions populations exist within a realised niche, primarily determined by environmental variables, their fundamental niche, but then further constrained by biotic interactions (Darwin 1859); greatest abundance is reached at the centre and uniformly decrease in density towards the edges (Sagarin and Gaines 2002). The range of a species obviously overlaps with that of many others, but Gause’s competitive exclusion principle (1934) states that species competing for similar resources will either drive one of the pair extinct, or evolve separate functional niches. This may result in contact zones, or overlaps where increased competitive behaviour may be observed. This has been demonstrated in playback experiments where recorded bird calls of one species stimulated increased response from its higher elevation competitor in areas near their contact zone (Jankowski et al. 2010). Finally, Haldane (1956) added to this an understanding that gene flow from the abundant centre of a population could explain why range margins fail to adapt to the unsuitable conditions beyond them; as local adaptation at the range margin may be diluted by a large influx of unadapted individuals.

As our understanding of range dynamics has grown, established theories have been challenged. Examples of this include a disputation of the abundant range centre, suggesting that populations are rarely most abundant at the centre of their distribution (Sagarin and Gaines 2002, Tuya et al. 2008) and expansion of our understanding of ecological genetics and gene flow concerning the dynamics of source-sink environmental heterogeneity, which considers how ecological traps affect the adaptive value of certain traits (Sexton et al. 2009). Whilst all traditional models of niche dynamics suggest competitive exclusion must occur to some degree, and there are some classic examples, such as Zaret and Rand’s observations of seasonal coincidence non-competing river fish (1971), in some of the most biodiverse regions of the planet such as tropical forests many species apparently coexist without obvious niche partitioning (Leigh et al. 2004). Such observations led to the development of neutral theory, in which species were assumed to be functional equivalent (Hubbell 2005). Although neutral theory does not purport to disprove niche difference (Hubbell 2005), it questions how useful and meaningful it is to models of species distributions and works as a null- or counter- hypothesis to competitive exclusions (Rosindell et al. 2011) and in practice is often remarkably difficult to disprove (Ricklefs 2006). Similarly, the focus on environmental conditions in studies of species distributions may have come at the expense of developing understanding of how biotic processes shape species’ ranges. Biological causes many underlie distributions that appear to be environmentally determined.

For example, one study found that the temperature sensitivity of avian blood parasites was found to contribute to the limitation of many montane Australian bird distributions at their warm edge (Zamora-Vilchis et al. 2012) in a manner that could be mistaken for direct environmental limitation. As an increasingly holistic approach is applied to ecology, the contribution of biotic causes to range limitation will need to be more broadly understood.

Developing and validating these models has been conceptually and practically challenging due to the complicated nature of species ranges. Distributions are heterogeneous and fluid in nature, boundaries move over time (Faille et al. 2010) and low survey resolution may fail to pick up fine scale delineation of ranges (Inouye 2005). As such range limits require contextualisation within a spatial and temporal scale. Even defining the distribution of a single population may be difficult due to migration, movement, or sampling limitations; after all, the absence of a species record is not the same as absence of the species (MacKenzie 2005, Beale and Lennon 2012). Equally, the presence of a species in an area may not indicate that it is capable of maintaining positive population growth (Battin 2004). Suitable habitats that remain unoccupied may require detailed investigation to explain (Lane et al. 2001, Tajek et al. 2011), or may currently elude explanation, revealing gaps in our understanding (Wild and Gagnon 2005). Clearly there are practical and theoretical obstacles that complicate the study of range limits, but there are also valuable insights to be gained from the field. The importance of range limits and the complexities of their study have ensured the topic’s persistence as a popular area of research.

Efforts to validate ecological theory concerning range limits have often used ecological gradients to compare how limits are determined under differing ecological stress (Crain et al. 2004, Sanford et al. 2006, Normand et al. 2009, Gifford and Kozak 2012). Stress here refers to biological or environmental factors that negatively affect a target species’ fitness or reproductive productivity. Conditions that are stressful for one species may not be stressful for all, but certain stresses may affect species more generally than others. Many of these studies seek to clarify how biotic and abiotic factors interact to determine range limits (Crain et al. 2004, Gifford and Kozak 2012, Jankowski et al. 2013) as low stress range limits have been theorised to be set by biotic interactions, such as competition, more often than high stress limits (MacArthur 1972). The theory has been gradually refined following stress gradient studies such as Connell's classic work on littoral zonation (1961) that demonstrated the importance of desiccation stress at the upper limit of the study species with competition mediated zonation determining range boundaries when desiccation stress is low (Connell 1961). Generally, it is appreciated that the relative importance of biotic and abiotic factors, in determining where distribution limits are set, varies across a stress gradient: at high stress limits, such as poleward, high elevational, high desiccation, or high salinity limits; the environmental stress is most likely to be the factor preventing species expanding their range. At low stress limits, such as warm limits, or other suitable conditions to a species, the importance of environmental conditions in setting species distributions is lessened and biotic interactions such as competition become increasingly important (Normand et al. 2009). Competition is commonly noted as an important biotic interaction that limits species distributions (Crain et al. 2004, Kissling et al. 2012, HilleRisLambers et al. 2013), but predation, herbivory, disease, parasitism, mutualisms and facilitators are also important (Schemske et al. 2009, Kissling et al. 2012, HilleRisLambers et al. 2013).

Our work focuses on the elevational stress gradients experienced by avifaunal communities in tropical montane systems, which appear to be under-represented in the literature (Thomas 2010, Cahill et al. 2014). Although studies of tropical montane environments are not uncommon (Williams et al. 2003, Raxworthy et al. 2008, Chen et al. 2009, Staunton et al. 2016), much work is required to ensure the diversity of tropical montane biomes are represented. There have been numerous mechanisms suggested to explain why we might expect avifauna to experience stress at high elevations, including thermal stress and hypoxia (Jankowski et al. 2013), although temperature is usually regarded as the most important determinant of upper limits of latitudinal gradients (Schemske et al. 2009). Explanations involving biotic interactions may explain the zonation and species replacement along elevation gradients that is commonly found in tropical montane communities, as indicated above in bird call playback experiments looking at behavioural responses of competitors at the range margins (Jankowski et al. 2010). Further investigation into the importance of biotic interactions on lower distribution limits of species may improve our understanding of zonation. The relative importance of biotic interactions may even be greater in tropical systems when compared to temperate ones. Empirical work on temperate and tropical, sessile marine invertebrates has shown that the strength of both predation and biotic resistance to invasion is stronger in tropical communities (Freestone et al. 2011, Freestone et al. 2013). Furthermore, a review of studies examining the importance of various biotic processes, including predation, mutualisms, and indirect effects, found biotic interactions to be of greater importance or strength in the processes at tropical sites, when compared to temperate ones in most cases (Schemske et al. 2009). Work in which the shift of upper elevational limits and high-latitude limits were compared for 40 avian species, has indicated that elevational and latitudinal temperature gradients may react differently to changing environments (Auer and King 2014), suggesting that conclusions regarding the proximate causes of latitudinal range limits may not hold true for limits across and elevational gradient.

The tropics may also face different challenges from climate change than are faced in temperate systems, such as lowland attrition, where species loss from extinctions will not be replaced by new species as there are no warmer habitats from which to source replacement species (Colwell et al. 2008). Tropical montane systems are also under threat as upward range-shifting species are at risk of shifting into a dead-end with no more space to expand, as their range gets constrained from below (Jankowski et al. 2010). Species in tropical communities have been generally shown to inhabit narrower thermal niches than temperate species (Cadena et al. 2012, Urban et al. 2012) and may exist closer to the margins of this niche than temperate counterparts (Deutsch et al. 2008); with generally more restricted ranges on mountains, tropical montane species may be at greater threat than their temperate counterparts (Urban et al. 2012). To predict how these species will react in the future we need to understand the degree to which the lower and upper distribution limits are determined by biotic interactions and abiotic processes (Jankowski et al. 2010, Gifford and Kozak 2012). Will contraction of species ranges be due to increasing temperatures or by competitive species also escaping from warming? Furthermore, if biotic interactions are generally responsible for range limits, how will lowland attrition change the process by which distributions are constrained? If there are fewer species range shifting into montane systems, will warm limits change in the same way? The need for further work in the tropics is apparent: this thesis adds to this area of the literature.

Despite theoretical work and widespread agreement predicting biotic interactions be more important than abiotic interactions at low stress distribution limits, reviews have been unable to support these conclusions with data. In general, the literature identifies abiotic causes to range limits in general (Sexton et al. 2009), although Sexton et al.'s review makes no comment on the relative importance of biotic interactions. Building upon this, Cahill et al. (2014) examined the literature concerning studies where the causes of warm low-stress limits of species were identified and determined that these low stress limits were most often determined to have abiotic causes. Although no reviews have directly compared how often biotic causes are attributed to high and low stress limits separately, leaving the possibility that the relative importance of biotic interactions in determining range limits remains greater at low stress limits, these results seriously challenge the classical view presented by MacArthur (1972). However, the evidence does not refute the importance of biotic interactions in determining low stress limits; they fail to find support for it. Cahill et al. (2014) stress that that many studies do not make efforts to test both abiotic and biotic factors explicitly and have a tendency to "support factors that were tested", meaning that alternative factor may still be important, and studies poorly represented tropical montane systems (2014), as has been noted elsewhere (Thomas 2010). In fact, range edges seem to be under-sampled, distorting our view of them (Sagarin and Gaines 2002). Overall, the complexity of theoretical models concerning range limits seems to be advancing much faster than the frameworks supporting experimental design, which may fail to capture data most important to testing predictions (Sexton et al. 2009). Further study is needed, especially concerning tropical and montane systems and their range limits. Careful planning is needed during experimental design to ensure data will be informative, explicitly testing multiple possible causes of range limits.

As our understanding of range limits has improved, it has informed developments in the field of species distribution modelling, as can be seen in the incorporation of biotic interactions into the models (McMahon et al. 2011, Kissling et al. 2012, Pickles et al. 2013, Wisz et al. 2013, de Araujo et al. 2014). Species distribution models have now become numerous, and have in important part to play in the future of biodiversity conservation (Mouquet et al. 2015). Despite improvements in the models in numerous areas there remain questions concerning the direction that the field should take. Some believe that there has been an overcautious suspicion of complexity in models, with a preference for simple models that were viewed as more generally applicable, intelligible, and communicable (Evans et al. 2013). Proponents of increasing model complexity may believe that it increases the accuracy of models and does not prevent models being generally applicable (Evans et al. 2013, Mouquet et al. 2015). The growing consensus, informed by numerous studies (Lavergne et al. 2010, Meineri et al. 2012, HilleRisLambers et al. 2013, de Araujo et al. 2014), is that including biotic interactions in species distribution models is an essential part of the field's evolution (Kissling et al. 2012, Wisz et al. 2013, Singer et al. 2016). There is also an acknowledgement that as these models develop theoretically at an increasingly rapid rate, there is potential for a gap to develop between them and the understanding of the stakeholders that use them (Mouquet et al. 2015). The consensus among reviews recommends increased validation of these models and the production and accessibility of multi-species datasets with larger geographic extents, consisting of multiple populations and more records (Araujo and Guisan 2006, Kissling et al. 2012, Wisz et al. 2013, Mouquet et al. 2015, Singer et al. 2016).

Our work focuses on the highly diverse Afromontane communities of the Albertine Rift region (Plumptre et al. 2007, Carr et al. 2013). We characterise and compare the distributions of the region's avifauna. The region has been identified as an Endemic Bird Area (BirdLife International, 2015) and recognised by the World-Wide Fund for Nature as its own ecoregion (WWF, 2015). It has a rich evolutionary history (Voelker et al. 2010), characterised by climatic upheavals in which mountains have played an important role in diversification. The mountains of the Rift will likely continue to serve as refuges in the future as moist islands in a drying landscape (Scheiter and Higgins 2009, Zhou et al. 2014), increasing the need for us to conserve the habitats found there. Establishing if and how climate change is affecting these systems is essential to planning for their conservation. In the second chapter of our work we attempt to document changes in the avian montane communities of the Albertine Rift.

Before analysing our data, understanding the recommendations made by previous work that have shaped the analysis is important. Empirical work has benefited from collecting data covering a significant proportion of a community, or a subset of a community (Williams et al. 2003, Chen et al. 2009, Cunningham et al. 2016) and future work should try to emulate this to increases the reliability of results. Studies have suggested covering a large geographic area, with multiple populations of the study species to ensure that results are generally true for a species rather than a population (Wisz et al. 2013). Work should aspire to collect data at a fine-scale resolution to address data gaps (Wisz et al. 2013). Cahill stresses the importance of considering both abiotic and biotic explanations explicitly to avoid a bias in results (Cahill et al. 2014). There is also a recognised bias towards studies of temperature (Cahill et al. 2014), despite the importance of rainfall in these systems (VanDerWal et al. 2013). The difficulty of gathering rainfall data in the tropics, especially in remote or mountain areas is considerable and direct measures of precipitation across the different elevational gradients spanning the Albertine Rift has not been pursued by local national park services. As such we have been unable to gather suitable rainfall data covering our study area. Precipitation is very high year-round throughout this region, nevertheless we recognise that low moisture availability can be a considerable stress at lower elevations in some systems. Without quantifying it, we are unable to determine the importance of precipitation in limiting these systems and it may be responsible for range shifts that deviate or even shift opposite to our general expectations (VanDerWal et al. 2013).

To understand even a single aspect of range limits in tropical regions such as the Albertine Rift, we need to bring together disparate stands of knowledge from multiple research areas. The need to understand the relative importance of biotic interactions in range limit determination has a clear academic basis, founded in classic works of ecology. However, the work has applications of pressing importance in improving the conceptual framework upon which species distribution models will be built upon and then simplified around. In the Albertine Rift, understanding how changes have already occurred and predicting the future of the region is a top priority for all stakeholders. Given the widespread support for large, multi-species dataset analysis in tropical montane systems, this work is both timely and important.

Chapter 2: The importance of biotic interactions in determining range limits within the avifauna communities of the Albertine Rift

2.1 Introduction

Understanding why a species occurs where it does and nowhere else is one of the fundamental questions of ecology (Gaston 2009, Normand et al. 2009). Answering this for even one species may require understanding patterns of movement such as dispersal and migration; disentangling interspecific interactions such as competition, mutualisms, or predation and characterising environmental gradients such as thermal or moisture limits. Ultimately, what determines a distribution limit must be explained in terms of mortality and fecundity (Lavergne et al. 2010). In short, individual species distributions must be determined by abiotic factors, biotic interactions, and historic accidents to varying degrees. However, the diversity of perspectives from which to approach the topic means that developing a comprehensive framework for understanding species distributions is complex (Gaston 2009). Developing a sophisticated understanding of distributions is becoming increasingly urgent as we attempt to adapt to environmental change, but this is hindered by the general lack of understanding concerning the degree to which the various possible causes of a species' distribution work together to determine its range (Araujo and Guisan 2006, Gaston 2009).

One central, yet insufficiently understood, research area concerns the relative importance of biotic and abiotic factors in determining species distribution limits (Normand et al. 2009, Louthan et al. 2015, Singer et al. 2016). Iconic studies, such as Connell's work (1961) on intertidal zonation have highlighted how biotic and abiotic determinants of distribution limits may vary asymmetrically in importance over a stress gradient; with biotically determined limits, such as those determined by competition, being more common in a lower stress environment. Subsequent empirical work has expanded to consider a variety of stress gradients, including salinity (Crain et al. 2004) and temperature, both across elevational (Bird and Hodkinson 2005, Ettinger et al. 2011) and latitudinal gradients (Normand et al. 2009, Cunningham et al. 2016). Results have generally related to too few species to indicate broad applicability (Bird and Hodkinson 2005, Ettinger et al. 2011), shown mixed results (Cunningham et al. 2016), or tested the theory indirectly, such as by evaluating the fit of environmental niche models at high and low stress boundaries (Cunningham et al. 2016) rather than investigating the mechanisms that may bring these trends about. The paucity of studies that separately analyse high and low stress limits means that much of the work in the field of range limits cannot be used to validate theories relating to the relative importance of biotic interactions across a stress gradient.

Despite strong evidence of biotic factors determining range limits in previous work, abiotic causes of range limits are more frequently supported in the literature than biotic causes or mixed biotic and abiotic causes, as demonstrated in a review of the causes of range limits in 146 studies (Sexton et al. 2009). Despite this, final conclusions relating to the importance of biotic interactions in determining range limits across high and low stress conditions are not yet possible. When warm, low latitude or low elevation limits have been examined separately from high latitude/altitude limits, the majority of warm-range limits still correlate with abiotic conditions as well as upper limits, contrary to expectation (Cahill et al. 2014). These studies strongly indicate that low-stress range limits are predominantly determined by abiotic interactions, however a number of limitations of range limit studies need to be addressed: previous studies generally did not differentiate between high and low stress limits and more commonly test for abiotic causes than biotic ones (Cahill et al. 2014). Cahill *et al.* (2014) stated that as studies tended to support causes that they investigate and often did not explicitly test for causes other than those they are investigating; previous work may have failed to identify the true causes of limits; especially if the cause was biotic or involved the interaction of biotic and abiotic factors. Cahill *et al*. (2014) indicated that future work should consider not only biotic and abiotic causes, but make efforts to determine the proximate causes of range limitation, not just associations and ultimate causes. However, as we only examined warm range limits, we were unable to comment on the relative importance of biotic interactions at low stress and high stress limits, leaving the possibility open that at low-stress, warm limits, biotic interactions are relatively more important determinants than at high-stress, cold limits.

Although the tropics are biologically rich and montane systems are often considered the most at risk from climate change (Urban et al. 2012), comparatively few studies have been conducted in the tropics examining montane range limits. Good studies exist from Australia (Williams et al. 2003, Staunton et al. 2016), Borneo (Chen et al. 2009), Madagascar (Raxworthy et al. 2008), and other locations, but the central Afromontane tropics, among others, are underrepresented given their diversity. Additionally, the existing tropical montane studies poorly document lower range limits (Thomas 2010). Overall this reflects a geographic bias in study location towards temperate systems (Thomas 2010, Cahill et al. 2014) and away from montane environments (Cahill et al. 2014).

We have yet to comprehensively describe species distribution limits and their changes for many tropical ecotypes in Africa, Asia, and South America. This is troubling as predation, biotic resistance to invasion, and many other biotic interactions appear to be stronger in the tropics (Schemske et al. 2009, Freestone et al. 2011, Freestone et al. 2013). The increasing strength of biotic interactions towards the tropics, along the thermal stress gradient, is an important assumption of one of the contending explanations of the elevated diversity at the tropics (Schemske et al. 2009). The increased importance of biotic interactions in the tropical biome is thought to have stimulated diversification, and the prevalence of this theory may partially explain why the implicit understanding that biotic causes underlie low-stress limits is so widespread, despite referring to a separate phenomenon.

There is widespread recognition that the importance of biotic factors in determining range limits increases at low stress distribution boundaries compared to high stress boundaries (Hampe and Jump 2011), and observations that including biotic interactions in Species Distribution Models (SDMs) can improve their accuracy (Meineri et al. 2012, de Araujo et al. 2014). However, our understanding of the importance of competition, predation, parasitism, and other interactions on the setting of high and low stress range limits has never been fully synthesised. Previous work has highlighted the importance of gathering information on large portions of an ecological community in order to ensure work has broad applicability (Williams et al. 2003, Chen et al. 2009, Normand et al. 2009, Freestone et al. 2011, Cunningham et al. 2016) along with a need for studies spanning a large geographic area, including multiple communities and multiple species within them (Wisz et al. 2013).

Here we investigate the relative role of biotic interactions in determining higher elevation cold limits and lower elevation warm limits for avifaunal communities in the Albertine Rift. We follow the definition of the area broadly defined in Plumpltre et al. (2007); consisting of areas surrounding the western branch of the East African Rift within the countries of The Democratic Republic of Congo, Uganda, Rwanda, Burundi, and Tanzania. The area encompasses numerous montane systems that offer replicate elevation gradients with varying avian communities. Rather than focus on a single species, we model the distributions of 349 species to identify, where possible, the cold and warm limits of their distributions. Avifauna are well suited for studies of this nature as an experienced surveyor can identify individuals from a large area quickly and accurately (Mac Nally et al. 2004). Across the Rift, these communities vary in habitat type from tropical savannahs to glacial peaks. Many species are endemic to the region as a whole, but also to locations within the rift. If it is correct that colder limits are mostly determined by temperature (Normand et al. 2009), but warmer limits are more likely to be determined by biotic interactions; and we expect thermal stress to increase with elevation, but species composition to vary greatly between communities; it is reasonable to expect that the cold limits of a species distribution will vary little across montane ecosystems in a region, whereas the warm limits may vary to a greater extent as the biotic interactions occurring changes. Consequently, it should be possible to test theories about the importance of biotic interactions at cold and warm distribution limits by assessing the variation between species distribution limits across multiple communities. Other stress gradients may affect distribution limits across elevation in the opposite direction, such as high temperature stress or low moisture availability. These stress gradients might also reduce diversity by limiting distributions. These would be plausible reasons to expect abiotic stress to be higher at low elevations, but we have reasons to believe that cold temperature stress is more important in our study. Low moisture stress is not likely to be an issue in this region due to extremely high rainfall throughout the year. Additionally, although high temperatures may lead to overheating, limiting some species low elevation distributions, this is believed to be generally less important than cold temperature stress (MacArthur 1972, Wiens 2011). It would be very unexpected to observe lower diversity at low elevations, but this might indicate that moisture or high temperature stress is playing an important role in these systems. If warm limits are more variable than cold limits and this variability correlates strongly with species richness, we might conclude that species interactions are related to changes in the elevation of distribution limits. We hypothesise that across montane ecosystems with similar environmental conditions, but varying community composition, generally the variation in elevation of a species' lower range limits across different communities will be greater than the elevational variability of their upper range limits. We also hypothesise that this trend will remain when range limit elevation is substituted for the estimated temperature of range limits, directly testing the importance of temperature stress in determining distributions.

After testing for differences in the overall variation between communities at the cold or warm limits of distributions, we seek to explain that variation between sites in terms of the variation between landscapes in lapse rates, species richness, forest cover, and maximum survey elevation (of forested sites). Lapse rate is a measure of how temperature changes with elevation, species richness is used as a proxy for the number of biotic interactions, and maximum survey elevation is assumed to be indicative of the maximum elevation of suitable habitat of the area visited. We predict that, if temperature is the main limiting factor at species' cold limits, we will find negative relationships between lapse rates and cold limits. This is because a low lapse rate indicates warmer temperatures at higher altitudes and so species would be able to survive at higher elevations. We expect no relationship or a lesser negative relationship between lapse rate and the elevation of species lower limits, as high temperature is not thought to be the proximate cause of the lower limit of species' distributions. If lack of suitable habitat is a limiting factor, we expect cold limits to positively correlate with landscape's upper forested habitat boundary. We expect a close correspondence between the extent of suitable vegetation (forest habitats) in a landscape, and the elevational extent of survey data, though this was not statistically tested. We expect species richness to have no meaningful effect on the upper limits of species distributions, but to positively correlate with the lower limits of a species distribution, as we expect increased species richness to indicate more biotic interactions and therefore a higher chance of a range-limiting competitor to be present at lower limits. When we substitute elevation, an indirect measure of temperature stress for the predicted temperature of limits, a direct measure of this, as the dependent variable in the linear models we expect the relationships to be reversed, as high altitudes have low temperatures. We attempt to explain observed variation in elevational limit using the landscape-specific variables of lapse rate, maximum elevation of forest cover, and species richness. Where most species have large relationship coefficients between limit elevation and an independent variable (such as species richness), that variable may partially explain the observed variation. If biotic interactions are the proximate cause of lower limit determination, we would expect the median relationship between lower distribution limits and species richness to be the largest of the variables.

2.2 Methods

2.2.1 Study area and Landscape definitions

The Albertine Rift is a global conservation priority (Brooks et al. 2001, Plumptre et al. 2007) with extremely high rates of endemism. It is identified as an Endemic Bird Area (BirdLife International 2015) and an ecoregion by the World-Wide Fund for Nature (WWF 2015). It is thought to contain more endemic mammals and birds than any other area in Africa (Plumptre et al. 2007, Carr et al. 2013, Foden et al. 2013). The Albertine Rift contains a number of unique montane landscapes with varying community compositions. The Wildlife Conservation Society conducted 17,500 ornithological survey points in The Albertine Rift region between 2001 and 2016 (Plumptre et al. 2002, Owiunji et al. 2005, Plumptre et al. 2009, Plumptre et al. 2010), from which we selected our data. We used a subset of these data, identified on the ground as falling within Afromontane forest, consisting of 6897 points.

We defined 10 landscapes within the Albertine Rift that cover the survey data collected by the WCS by using smoothed ASTER DEMs to approximate the perimeter of the downslope area of mountainous regions and grouping the resulting boundaries into coherent landscapes. This allowed us to separate well known regions such as the Ruwenzori Mountains and the Murchison-Semliki landscape (Fig.1).

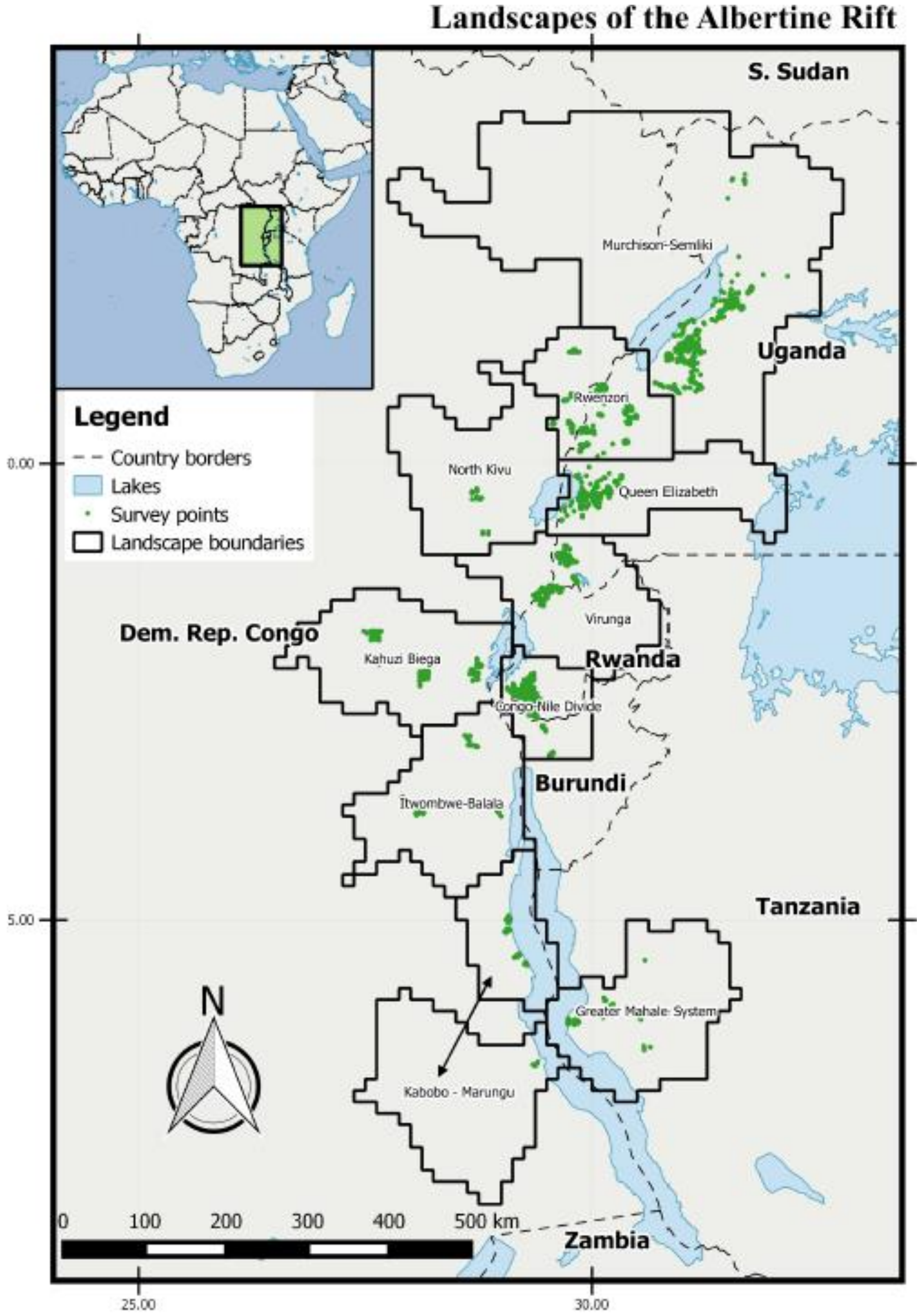


Figure 2.1. The landscapes of the Albertine Rift, identified from smoothed DEMs of the region, are shown in thick, black, solid lines. Green dots indicate survey points.

2.2.2 Survey Methods

Two survey teams undertook the majority of surveys, operating throughout the 16 years of data collection. During that time, they visited all major forests and protected areas at least once. They conducted point counts every 250m along altitudinal transects of variable length, depending on the extent of the forested area of sites. Before conducting a survey, teams waited for three minutes from arrival to allow avifauna to recover from disturbance. Point counts lasted five minutes, during which they identified all individuals seen or heard to species level and recorded the point's location, altitude and broad habitat type.

Point elevation data was absent for 423 records. We estimated the elevation of these points from ASTER Digital Elevation Models (DEM) (LP DAAC 2009a) using the site co-ordinates. We used the SRTM 90m Digital Elevation Database (Jarvis et al. 2008) at a 90m scale to predict lapse rates and forested habitat limits in altitude.

2.2.3 Climate data

In order to classify months into wet or dry and hot or cold months we identified seasonal changes separately for each landscape; classifying months into wet or dry categories depending on whether their mean precipitation was greater or less than the mean precipitation of all months combined, and hot or cold depending on whether the mean temperate was above or below the mean temperature of the landscape for all months. We determined patterns using two monthly, long term datasets: precipitation data from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) dataset (Funk et al. 2014) at 0.05° spatial resolution from 2001 to 2016 and temperature data from the Climate Research Unit's (CRU) dataset: CRU TS v3.23 (Harris et al. 2014), at a 0.5° spatial resolution from 2001 to 2014.

To explain the variability of the species' range limits across different communities we calculated lapse rates using MODIS Land Surface Temperature (LST) data (LP DAAC 2009b) for each season following Maeda (2014), based on data from 2008. Unlike Maeda (2014), we used only a single year's data and so could not average values across years to remove additional data based on cloud cover. Temperature is used in our analyses on a relative scale and, assuming that day and night temperatures correlate, we do not believe that the choice between them will have a meaningful effect on our results. If there is a poor correlation between day and night temperatures, then we may be incorrectly estimating the effect of temperature. This might result in an underestimation of the effect of high temperature stress at lower limits. However, due to the effect of albedo on day time temperatures we were unable to determine if this is the case. Night time temperature satellite data is less susceptible to the effects of albedo and so can produce a more accurate estimate of lapse rate (Maeda 2014).

We estimated the lapse rate in each landscape by fitting a linear model to the relationship between night time temperature (LP DAAC 2009b) and altitude (Jarvis et al. 2008) within a landscape and for each season. Due to lower confidence in temperature at given GPS coordinates, we predicted the night time temperature of sites based on the lapse rate and recorded altitude of points.

2.2.4 Forest cover and species richness

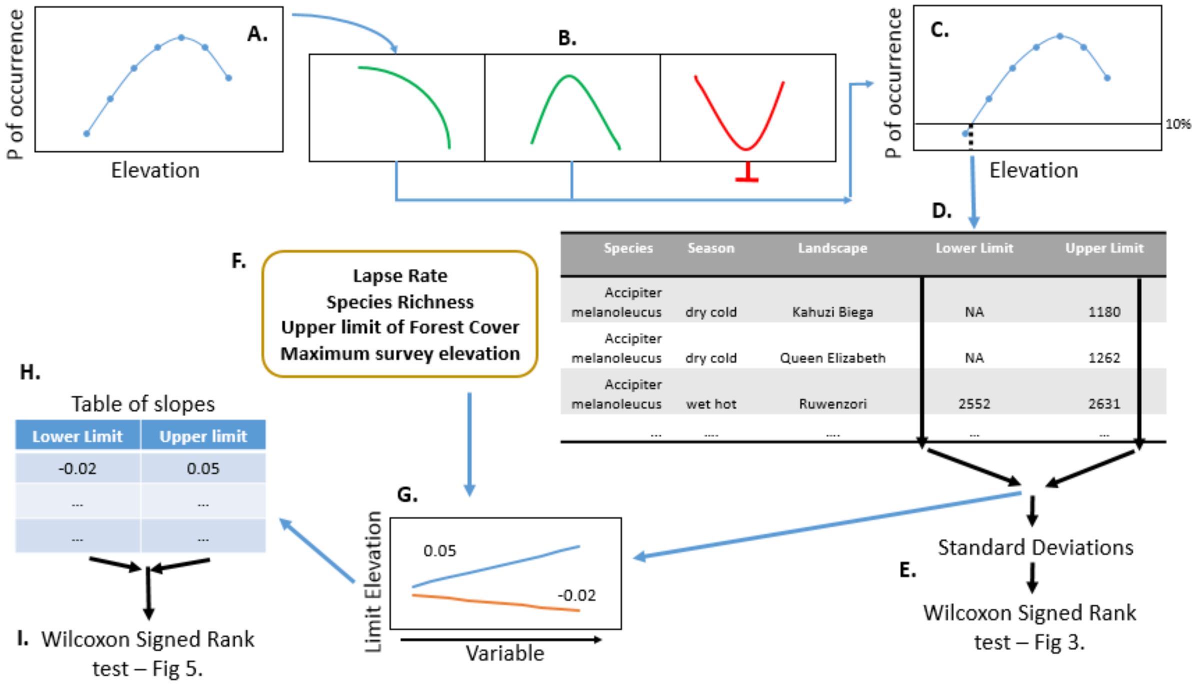
In addition to lapse rate, we also calculated forest cover and species richness. We determined the upper boundary of suitable forest cover for each landscape using vegetation maps generated by the WCS from aerial photographs and satellite imagery (Akwetaireho et al. 2010, Plumptre et al. 2014), along with unpublished WCS vegetation maps generated using similar methods. We aggregated the maps to a resolution of 250m and classified the vegetation into forested and non-forested locations. We follow the example of previous work (Mason et al. 2015) that cushioned the effect of spatial outliers on setting range margins by averaging the 10 most extreme distribution values, though we implement a slightly different method. To avoid extreme outliers, we defined the forest limit as the altitude of the 10th highest and 10th lowest cell with suitable forest habitat. We estimated the species richness of each landscape using the Chao diversity index (Chao et al. 2005) generated using the R function *specpool* in the package *vegan* (Oksanen et al. 2016); this function estimates true species richness using a probabilistic approach based on the chance that two individuals, randomly chosen from two survey points, are of a species shared between the two locations (Chao et al. 2005).

2.2.5 Predicting species distribution limits

Because species absence from a point survey does not necessarily mean true absence from an area (Beale and Lennon 2012), we estimated the probability of a species occurring at a given altitude within a landscape using Generalised Additive Models (GAMs) (Wood 2011) to predict the probability of a species occurring at a given elevation or at a given predicted temperature based on the landscape and lapse rate. GAMs are recommended for predicting species distributions (Meynard and Quinn 2007) as they allow the data to determine the shape of the relationship between a variable and the data, rather than assuming a certain relationship *a priori*, allowing the fitting non-parametric relationships (Yee and Mitchell 1991). As many Afromontane bird species show seasonal altitudinal movements, we fitted separate GAMs to site occupancy data for each species with landscape and seasonal information (whether the month was a wet or dry month, and whether it was a hot or cold month) as independent variables. GAMs modelled the probability of species occurrence at a site given the landscape the site was present in and seasonal information based on two terms, one indicating whether the month of the survey was classified as wet or dry, another for whether it was hot or cold, as outlined above. These were included as factors. Three smooth terms were added, each with three degrees of freedom ($k = 3$). The terms were a function of the effect of elevation on presence based on the factor of landscape, wet/dry or hot/cold – the same factors as the predictors above. When no variability existed in one of these factors both the factor and smooth term was dropped from the GAM. If there was no variability in the factor landscape, no further analysis was undertaken as the species then cannot provide information about the variability of distributions cross landscapes. A binomial distribution was used. We sense checked predictions for biologically implausible response functions that may be generated for species with small datasets, this consisted of removing U-shaped predictions, that occurred in less than 4% of cases, from further analysis. We did not model distributions for species with fewer than five records. This was chosen maximise the number of range limits included for analysis using the strength of this dataset. Nearly 68% of the predicted distributions were for species with more than 30 records. We acknowledge that some species' predicted distributions may have been imprecise. However, the process of determining range limits excludes those that fail to identify a clear limit within the data, adding a further step of quality control. Failing to include identifiable range limits of low occurrence species risks completely ignoring the range determinants of the species most at risk from external pressures and we decided against that option.

We used the predictions from the GAMs to estimate upper and lower range limits, identifying a limit where the probability of occurrence within a landscape dropped below 1/10th of its peak occurrence probability for the landscape (i.e. if we predicted a species' peak occurrence to be at 1000m, where we predicted it to occur at 40% of sites, then we would set limits at the altitudes where we predicted species occurrence to drop below 4%, if any existed within the surveyed range). This was conducted separately for each combination of species, landscape, and season. We calculated the standard deviations of both the upper and lower limits of a species' distributions across all landscapes within which it occurred, for each season. This allowed us to test the first hypothesis, that the variation in elevation of a species' lower range limits across different communities will be greater than the variability of their upper range limits, by using a Wilcoxon signed rank test to determine whether upper or lower limits were more variable across species. We repeated the analysis with estimated temperature values substituted for elevation values, enabling us to ascertain the degree to which elevational variation in limits across landscapes could be explained by the differences in lapse rate across those communities.

We attempted to determine the cause of range limit elevation variation by conducting linear models separately for both upper and lower limits, determining the response of range limit elevation to species richness, lapse rate, and the upper extent of forested habitat for each species. Finally, we conducted Wilcoxon signed rank tests to compare the relationship between each of these independent variables and limit elevation between lower and upper limits. If there was a significant difference in the relationships between a variable at each limit, this may point to the causes of range limit variability across landscapes. The outline of these methods is presented in Figure 2.



Species	Season	Landscape	Lower Limit	Upper Limit
Accipiter melanoleucus	dry cold	Kahuzi Biega	NA	1180
Accipiter melanoleucus	dry cold	Queen Elizabeth	NA	1262
Accipiter melanoleucus	wet hot	Ruwenzori	2552	2631
...	....	....	...	...

Lower Limit	Upper limit
-0.02	0.05
...	...
...	...

Figure 2.2. Analysis Infographic: **A.** Probability of occurrence over the survey range is predicted for species with over 5 records. **B.** U-shaped distributions are removed. **C.** Limits are set where probability of occurrence drops below 10% of the maximum predicted occurrence probability of the species in that landscape. **D.** This information is tabulated for each species, season, landscape combination. **E.** The standard deviations of species limits across landscapes were compared across upper and lower limits with a Wilcoxon Signed rank test. **F.** Predictive variables are collected for each site **G.** Linear models correlate these variables with upper and lower limits. **H.** These are tabulated for each variable (**I.**) and a Wilcoxon signed-rank test compares the effect at upper and lower limits.

2.3 Results

2.3.1 For predicated elevation limits:

We successfully fitted GAMs for the probability of a species' occurrence along an elevational gradient for 349 species across our ten landscapes. Of these species, we identified at least one range limit for 320 species. We required multiple predictions of a species' range limit across the landscapes to calculate the standard deviation of each species' upper and lower range limits. This reduced the number of species to 200, for which we separately calculated the standard deviation of both upper and lower limits by season. We found the median variation in elevation of upper limits to be significantly greater than that of lower limits in all seasons (V = 2423, 3562, 3321, and 3097 for dry/cold, dry/hot, wet/cold and wet/hot seasons respectively, p < 0.001 in all cases, Fig 3).

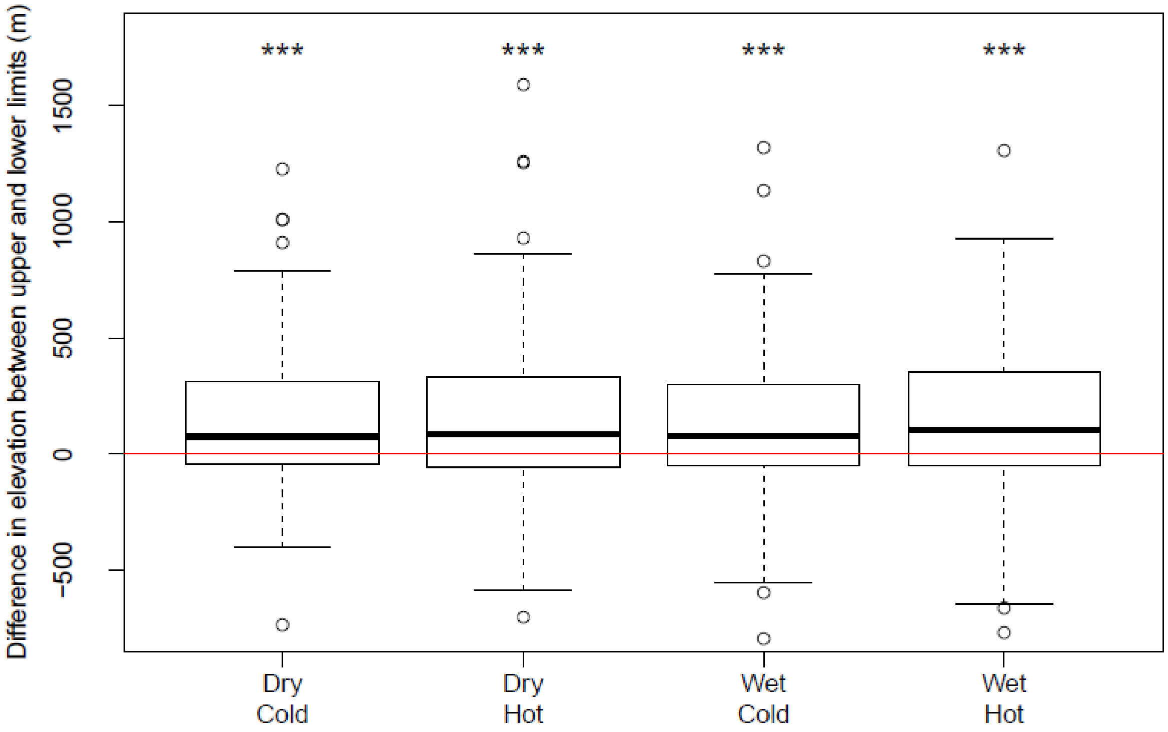


Figure 2.3. The difference between the amount of variation in upper and lower limits of species in elevation (m) for each season, where "***" indicates where p < 0.001. Data above the red base-line indicate species where upper range limits are more variable than lower range limits while the opposite is true below the red base-line. In all cases the median difference between the standard deviations of upper and lower limits shows upper limits to be more variable and is highly significant.

2.3.2 For predicted temperature gradients:

When we modified GAMs to model the probability of species occurrence along a temperature gradient we successfully fitted models for 344 species across the ten landscapes. We identified at least one range limit for 317 species, which reduced to 208 species for which the standard deviation of upper and lower limits could both be calculated when aggregated by season. We found that upper limits were significantly more variable than lower limits in hot seasons (Dry-Hot and Wet-Hot, V = 5434, p < 0.05, and V = 4972, p < 0.01 respectively, Fig 4).

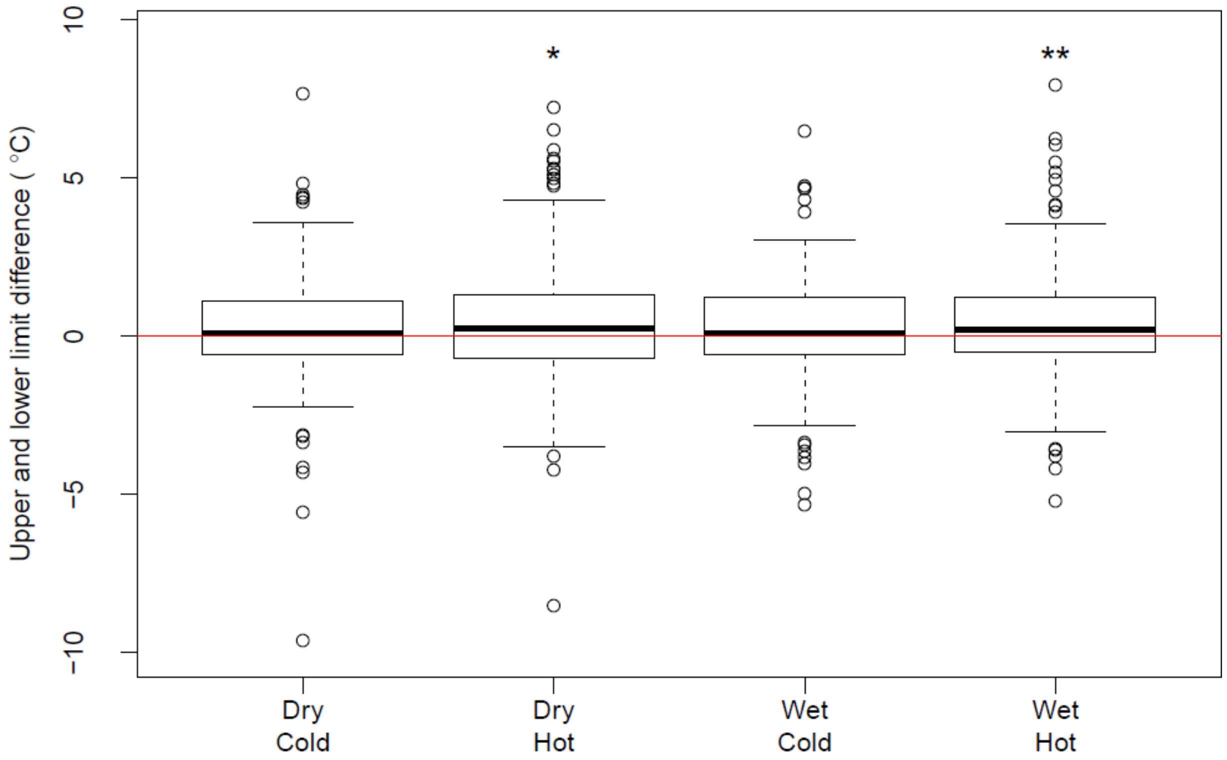


Figure 2.4. The difference between the amount of variation in warm and cold limits of species in estimated temperature (°C) for each season where "*" indicates where p < 0.05 and "**" indicates where p < 0.01. Data above the red base-line indicate species where upper range limits are more variable than lower range limits while the opposite is true below the red base-line.

2.3.3 Linear Models

We examined several possible causes of the variation between landscapes: lapse rate, species richness, extent of forested habitat and survey extent (a similar measure to forested habitat). This allowed us to investigate possible causes of range limit variability while testing our second hypothesis: that biotic interactions would be the most important determinant of lower range limits (i.e. that the effect size of species richness at lower limits would be higher than that of other predictors).

Linear models were conducted separately for upper and lower limits. The dependent variable, either limit elevation or predicted temperature was modelled in response to one of the specified independent variables, resulting in a separate model for each combination of limit (upper or lower) and predictor (lapse rate etc.). Each model contained one of the independent variables, species, and an interaction between the two. When we compared the relationship between upper and lower elevational limits and these variables, all variables except for the lower boundary of forested habitat acted significantly differently at upper and lower distribution limits (Table 1). When we compared temperature limits in this way, only richness and the lower boundary of forested habitat significantly differed in relationship between upper and low limits (Table 2). On average, we found over 450m difference between high elevation limits and over 250m between low elevation limits (Supplementary Data), with aerial photo derived forest limits being lower on average than survey limits (including only sites identified as being in forested habitats) in both cases.

Table 2.1: Wilcoxon signed rank tests on paired species relationship coefficients across lower and upper limits in elevation. The median relationship coefficient between a limit (response variable) and an independent variable are listed in the first two columns. The following columns describe the test results. Negative pseudo medians indicated that species' upper range limits generally have lower value relationships to the independent variables. All values have been scaled to allow direct comparison across all variables.

	Lower Limit Median	Upper Limit Median	V value	n	P	Pseudo median	95% Confidence Intervals	
Lapse rate	-10.31	12.86	5809	177	0.002	-63.04	-108.3	-21.48
Species richness	-62.11	16.91	3179	146	< 0.001	-106.1	-155.2	-59.65
Upper forested limit	-6.13	37.81	4137	146	0.016	-65.54	-122.7	-12.42
Lower forested limit	13.56	78.86	4543	146	0.108	-60.26	-156.2	12.07
Upper survey limit	1231.7	5287	86	146	< 0.001	-4052	-4111	-3996
Lower survey limit	546.7	1913	429	146	< 0.001	-1334	-1384	-1275

The direction of many of the relationships was unexpected (summarised in Table 1 and 2). Most species had negative relationships between limit elevations and both lapse rate and species richness for lower limits but positive relationships for upper limits. We found positive median relationships between upper and lower boundaries of forested habitat and their respective distribution limit, but lower boundary of forested habitat had an unexpectedly large, positive median relationship with upper distribution limits of species.

Table 2.2. Wilcoxon signed rank tests on paired species relationship coefficients across cold and warm temperature limits. The median relationship coefficient between a limit (response variable) and an independent variable are listed in the first two columns. The following columns describe the test results. Negative pseudo medians indicated that species' cold range limits generally have lower value relationships to the independent variables. All values have been scaled to allow direct comparison across all variables.

	Lower Limit Median	Upper Limit Median	V value	n	P	Pseudo (median)	95% Confidence Interval	
Species richness	0.438	0.148	8803	165	0.001	0.437	0.173	0.696
Upper forested limit	-0.243	-0.349	6904	165	0.927	0.009	-0.259	0.289
Lower forested limit	0.118	-0.134	8218	165	0.026	0.391	0.041	0.859
Upper survey limit	-0.756	-0.996	8245	165	0.023	0.339	0.042	0.591
Lower survey limit	-75.600	-45.080	319	165	< 0.001	-30.65	-30.94	-30.35

The strongest relationship identified was the positive relationship between the boundaries of survey elevations and distribution limits (Fig 5). Though significantly different between upper and lower distribution limits, upper and lower survey boundaries had a strong positive median relationship with all limits, with the strongest relationships found between upper survey boundaries and the upper limit of species distributions.

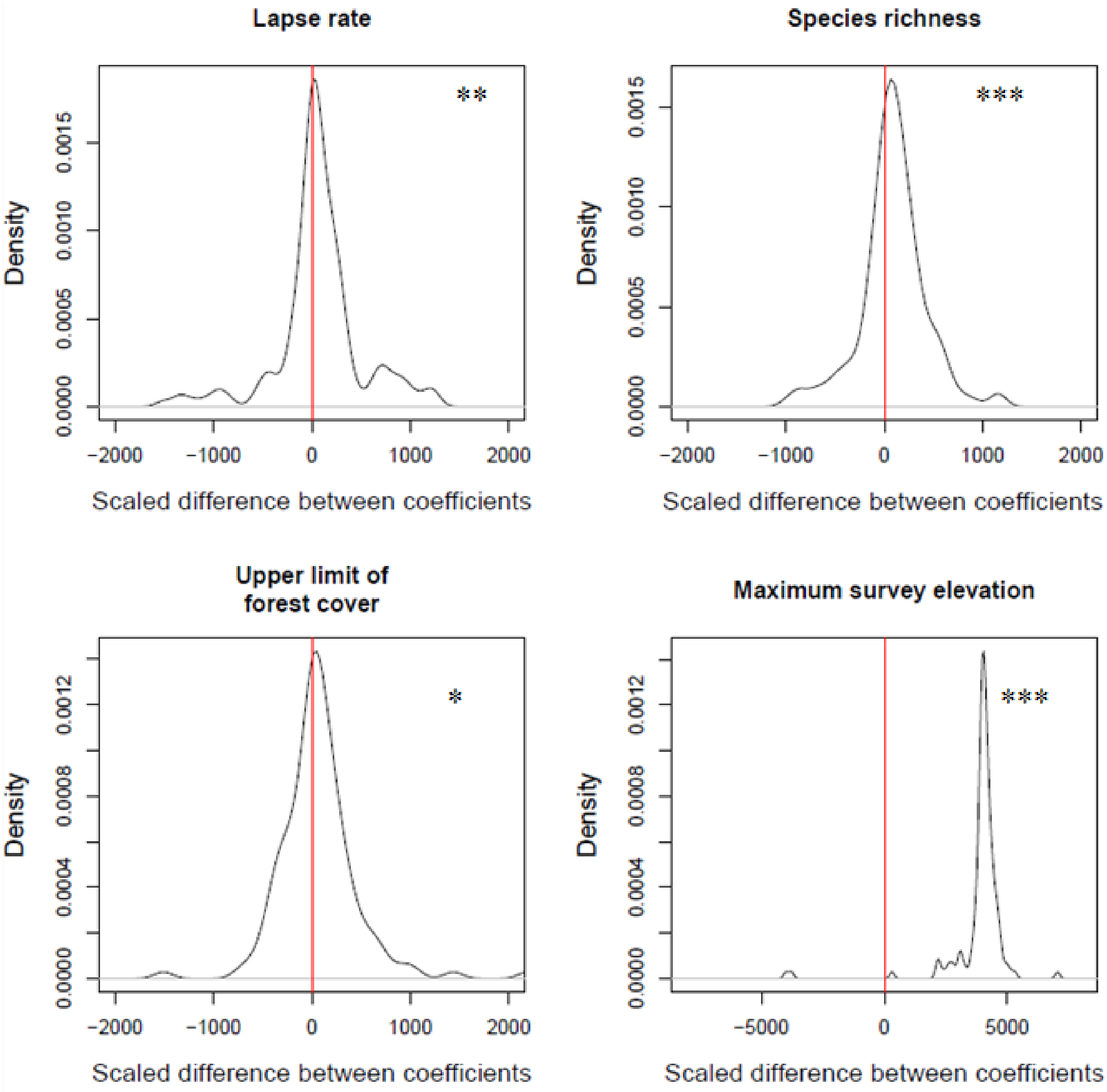


Figure 2.5. For each species, we determined the relationship coefficients between range limits and lapse rate, species richness, the upper limit of forest cover, and the maximum survey elevation. The difference between the values of these relationships at upper and lower limits was calculated for each species. These graphs show the distribution of those differences, where to the right of the red line, upper distribution limits have more positive coefficients than lower limits. The independent variables have been scaled to allow their direct comparison and outliers have been cropped. All show significantly different relationships exist between survey limits which may contribute to the difference in range limit variability between upper and lower limits. "*" indicated: $p < 0.05$, "**" where: $p < 0.01$, and "***" where: $p < 0.001$.

2.4 Discussion

We rejected our first hypothesis, that lower limits would be more variable in elevation than upper limits, and rejected the strong version of our second hypothesis, that the largest influence of lower limit elevation variability across landscapes would be species richness. However, we did find partial support for a weak version of this hypothesis, in that the effect of species richness was larger at lower limits than at upper limits. Traditional thinking on range limits has placed great importance on cold temperature stress in determining species distributions and is at the heart of classic explanations for biogeographical trends of species richness (MacArthur 1972, Wiens 2007). Cold temperature limits were highly variable in elevation and in their estimated temperature, indicating that cold temperature stress was not as important as other variables. We suggest that further work should focus on testing for the importance of cold temperature stress in range limit determination, both to maximise the predictive ability of species distribution models, but also to add to our understanding of stress in general.

We found no evidence of increased variability of lower distribution limits across landscapes than upper limits: indeed, we found the opposite to be true. This result was robust to seasonal differences, and persisted when we substituted the predicted temperature of limits for the elevation limit itself, though only during warmer seasons in the latter analysis. We are not aware of other studies that discuss the variability of species high and low stress range limits across multiple populations. We had predicted that a species' upper limits would not vary greatly across communities as the determining factor of upper limits, thought to be temperature (Jankowski et al. 2013), is relatively similar across landscapes. However upper limits were found to be more variable across landscapes. Lapse rate was variable across landscapes and resulted in different temperatures at equivalent altitudes across the study areas, but when these differences are accounted for, upper limits remain highly variable.

Although lapse rate and upper forested habitat boundary both account for some of the increased variability of upper limits (supporting both studies that indicate montane limits may be habitat dependent (Axmacher and Fiedler 2008) and those that stress the importance of temperature in determining montane limits (Jankowski et al. 2013)), the range of suitable sites (represented by the elevational bounds of suitable survey data from the landscape) seems to account for the greatest amount of variation between sites. As most species' upper distribution limits are far from the treeline, the mechanism determining this is unclear.

We found poor correspondence between the elevational extent of forested habitat and the elevational extent of surveys, though we found neither measure to consistently set forested habitat boundaries at a higher point across the study landscapes. At low limits, this is likely to reflect that although suitable habitats existed at lower elevations they may not have been connected to the national parks surveyed or near to the populations considered. The discrepancy may also reflect difficulties in classifying vegetation types from satellite and aerial vegetation data, however, this problem has received little attention in the literature and so is unlikely to be important (Xie et al. 2008). The vegetation maps were developed by teams with expertise and familiar with the areas' local environments.

Our initial expectations were that species' lower limits would generally be more variable across landscapes due to varying biotic interactions. Contrary to this, we found upper limits to be more variable, but most species' range limits correlated with species richness to a greater extent at lower limits, indicating that the effect of biotic interactions may be relatively more important at low stress limits. Species living in more species-rich landscapes tend to have larger altitudinal ranges, primarily due to expansion down the mountain, than when the same species lives in less diverse landscapes. We have used species richness as a proxy of interspecific competition, that is thought to narrow the elevational distributions of species (Jankowski et al. 2010). It is possible, that the addition of species is increasing the positive biotic interactions of avian species and facilitating wider elevational distributions (Travis et al. 2005). Despite some evidence that mixed species flocks have increased feeding rates (Hino 1998), there is little work that indicates that avian communities benefit greatly from directly mutualistic interspecific interactions.

Previous work on species area relationships has shown that, in habitats with a larger area, population size should increase (Wiegand et al. 2005) and it is possible that mountains with more available forested habitat increase species population and, as a result, distribution sizes: more individuals overall means detections at sites close to range limits where relative abundance is low are more likely than in landscapes where overall abundance is low. The effect of upper forested survey elevation is not related to temperature; the lapse rate and upper forested survey elevation do not correlate and the effect remained when range limits were calculated using predicted temperature.

Cahill *et al*'s work (2014) highlighted the importance of investigating the proximate causes of range limits. Although we did not identify the proximate causes of range limits, further work should build upon these results and consider species-specific proximate causes for distribution limits, especially for upper limits where much of the variability is unexplained.

Previous work also called for large datasets of multiple species and populations in a large geographic area (Kissling et al. 2012, Wisz et al. 2013, Mouquet et al. 2015) and we aimed to meet those criteria. We have treated lower and upper distribution limits separately and attempted to examine how biotic and abiotic variables vary in effect between them in line with the data utilised by Cahill *et al*. (2014). Though abiotic factors appear to dictate range limit elevation to a greater extent than biotic interactions at all range limits. Biotic interactions may still be relatively more important at low stress limits than at high stress limits as the effect size of species richness on distribution limits was greater for lower limits. Unexpectedly, the direction of this relationship meant that distribution limits were lower in species rich landscapes. We also found species' upper limits to be more variable over multiple landscapes than their lower limits, opposite to our expectations. This is only partially explained by temperature and species richness, possibly indicating that abiotic factors are highly important in determining low elevation limits. A large amount of this variation seems to be associated with the upper boundary of surveyed forest, possibly indicating the local availability of habitat as a key feature, though the proximate cause of this variation is unknown and requires further investigation.

Chapter 3: Range Shifts in the Albertine rift

3.1 Introduction

The world is facing potentially huge challenges in the form of global climate change and species extinction (IPCC 2014). Evidence the world over suggests that species are reacting to climactic events by shifting ranges to more suitable regions (Williams et al. 2003, Parmesan 2006, Sheldon et al. 2011), and how this dramatic shift will affect biodiversity is an ongoing question. Interest is being show in communities with nowhere to expand to, those on islands of suitable habitat such as those on mountains or near the poles, are at particular risk (Jankowski et al. 2010). Furthermore, ecosystems that stand to lose species in range shifts but have no species to replace them, such as tropical lowlands, are at risk of biodiversity attrition (Colwell et al. 2008). We ask; how is changing climate affecting the understudied Afromontane tropics and its diverse avifauna?

Our changing climate is providing numerous opportunities to observe how dynamic environments are shaped by the laws governing ecological systems. Range shifts are one such example (Sexton et al. 2009); describing the process by which species track two distinct waves of expansion and extinction across geographical space. At the leading edge, individuals colonise new areas and they are curtailed at the trailing edge by death or movement (Thomas 2010). There are opportunities to learn both as invasive species acclimate to their new surroundings (Ward and Masters 2007) and as previously suitable environments become inhospitable to their native inhabitants (Cahill et al. 2013). We stand to gain a substantial understanding of biological systems if the processes are documented well.

The challenge of planning for and managing the shifting distributions of species is a large logistical problem that is requiring increasingly sophisticated models of the process and of the environment (Araujo and Guisan 2006, Merow et al. 2014, Hipolito et al. 2015). Model validation requires access to large datasets that should cover large geographic areas, multiple populations, and multiple species (Wisz et al. 2013). Models should also be tested in different biomes to ensure that their results are broadly applicable, and parameters should be grounded in understanding based on similar communities to those being modelled. Improving the accuracy of predictions is of great importance as decisions made based upon them are consequential (Araujo and Guisan 2006, Jimenez-Valverde et al. 2008), affecting national management interests concerning the effects of species invasions, the viability of species relocations, and the likelihood of extinctions. Locally, conservation projects require reliable predictions, and stakeholders rely on natural resources for their ecosystem services and must plan for changes in their availability (Lawler 2009).

The biodiverse tropics and their montane systems are often considered the most at risk from climate change (Urban et al. 2012), but few studies of climate impacts have been conducted on tropical montane range limits. The underrepresentation of the tropical studies in the literature relating to range shifts (Thomas 2010, Cahill et al. 2014) may lead to the assumption that the montane tropics will behave no differently to their temperate counterparts (Thomas 2010). However, studies indicate an increased importance of biotic interactions at the tropics (Schemske et al. 2009, Freestone et al. 2011, Freestone et al. 2013) and considering our poor understanding of tropical lowland attrition (Colwell et al. 2008) there is a clear need for further groundwork. The central Afromontane tropics are unfortunately underrepresented in range shift literature, given their diversity. Although studies have been conducted in other tropical systems; examining threats to montane refuges Australia (Williams et al. 2003, Staunton et al. 2016), and montane range shifts in Borneo (Chen et al. 2009) and Madagascar (Raxworthy et al. 2008) to name a few; tropical montane studies remain in a minority (Cahill et al. 2014).

With that in mind, our work focusses on two Ugandan national parks: Mgahinga Gorilla National Park, first surveyed in 2004, and Rwenzori Mountains National Park, first surveyed in 2002. We resurveyed both national parks in 2016. Both parks fall within the Albertine Rift ecoregion of the East African Rift (WWF 2015), which is a highly diverse centre of endemism (Plumptre et al. 2007, Carr et al. 2013). The ecosystem services provided by the region are substantial and heavily relied upon by its inhabitants (Carr et al. 2013) and understanding how those may change in the future is important. Documenting existing range shifts is also needed. Understanding how species in regions such as the Albertine Rift are reacting to a changing climate is essential for planning their management and balancing future stakeholder interests (Carr et al. 2013).

We aim to determine if upper and lower distribution limits of species have generally changed between sampling periods. We hypothesise that both lower and upper distribution limits will have shifted uphill between the two periods. Over the duration of the study period we estimate a warming of 0.462˚C at Mgahinga Gorilla National Park and 0.652˚C at the Rwenzori Mountains National Park. Following the parks' gazetting in 1991 we suspect that the lowlands of national parks may have experienced some regeneration. Evidence of illegal mammal poaching was found throughout the parks and we do not believe that it has had an effect on our results. No logging was observed at the park, except for controlled cutting of bamboo by park rangers for local use, this is not expected to have affected our surveys. Previous work has recorded greater or more ubiquitous expansion of upper limits (Bergamini et al. 2009, Menendez et al. 2014). Reasons for this include the possible asymmetry between expansion and extinction, one requiring the colonisation of only a single individual, the other requiring the extinction of all individuals; or it may reflect the complexity of lower rang limit determination compared to upper limits. We hypothesise that range shift distance will be greater at the upper elevational distribution limits.

Species vary in both their vulnerability to climate effects and their capacity to disperse to mitigate the effects of change on their extinction risk (Foden et al. 2013). This can affect the rates at which species shift their ranges; species that are vulnerable to extinction contracting at the trailing edge of their distribution at a faster rate (Jiguet et al. 2007), and species with a higher capacity to adapt to change may decline slower (Foden et al. 2013). At the leading edge of a range shift, species with higher dispersal abilities will expand faster, and may have a greater capacity to withstand climate variation too (Foden et al. 2013). Certain functional traits of species are thought to strongly affect a species' ability to adapt or move when environmental change occurs (Jiguet et al. 2007). Previous work indicates that average mass may reflect extinction risk in mammals (Cardillo et al. 2005) and related measures such as body length have been used as a measure of susceptibility to extinction risk in birds (Trivino et al. 2013); although the mechanism by which this operates is not fully understood (Cardillo et al. 2005). Low clutch size has been associated with low evolvability (Foden et al. 2013) and susceptibility to climate change (Trivino et al. 2013) due to the inherently lower reproductive rate associated with the trait. Finally, forest dependency is associated with sensitivity to climate change due to habitat specialisation (Foden et al. 2013): species that are highly dependent on high quality forest are less likely to find appropriate habitats within the new suitable range. We hypothesise that these functional traits will explain differences in the rate of change of range limit elevations for species experiencing range limit shifts over the survey period. We expect a negative relationship between both species' forest dependency and species' mass when compared against the rate of range limit shift in elevation. Whereas we expect species' clutch size to positively correlate with the rate of range limit change experienced.

3.2 Methods

3.2.1 Survey area and methodology

The Wildlife Conservation Society collected these data as part of a series of ornithological surveys across the Albertine Rift to measure the biodiversity of these national parks (Plumptre et al. 2002, Owiunji et al. 2005, Plumptre et al. 2009, Plumptre et al. 2010). In both survey periods, the same team conducted point counts every 250m along altitudinal transects of variable length, depending on the extent of the forested area of sites. Full details of the survey methodology are provided in Chapter 2 Before conducting a survey, teams waited for three minutes from arrival to allow avifauna to recover from disturbance. Point counts lasted five minutes, during which they identified all individuals seen or heard to species level and recorded the point's location, altitude, and broad habitat type. We revisited and resurveyed previously surveyed points at Mgahinga Gorilla National Park and the Rwenzori Mountains National Park using a Garmin 60CSx GPS to ensure a close proximity to points. We conducted resurveys as close as possible to the coordinates of the previous points (Figure 1 and 2) using the same methodology. The same bird identifier was used in both surveys, with the possibility that his ability has improved over the study period, however both surveys were supported by other ornithologists during and following surveys to ensure that all surveys were conducted to a high standard. The original data consisted of 61 locations within Mgahinga Gorilla National Park and 201 locations within Rwenzori Mountains National Park. We resurveyed 59 locations in Mgahinga Gorilla National Park and 197 locations in the Rwenzori Mountains National Park (Figure 1 and 2). Due to logistical constraints, I was unable to conduct the repeat surveys at the same time of year as the previous work, this is discussed further below.

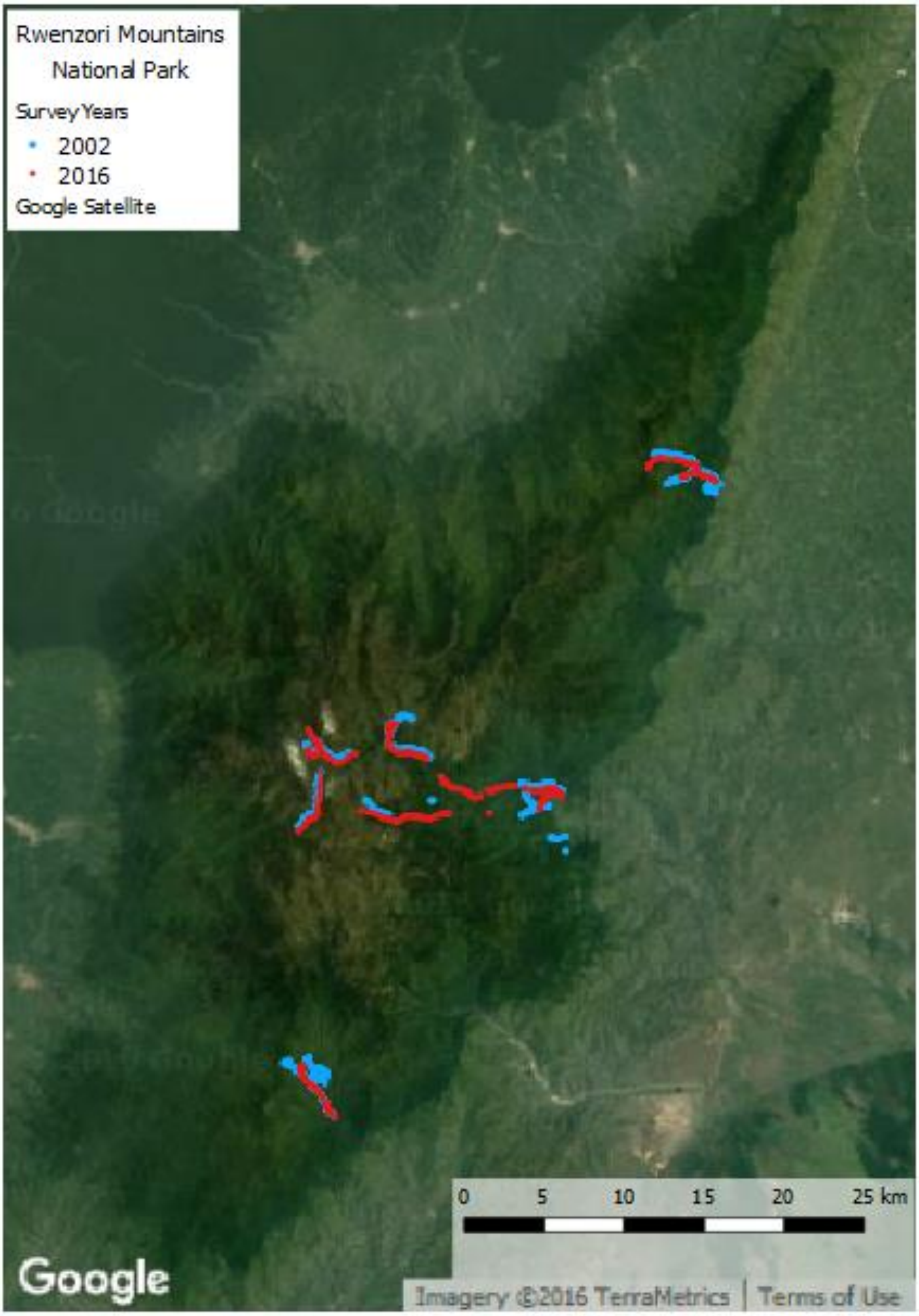


Figure 3.1. Locations of surveys conducted in the Rwenzori Mountains National Park

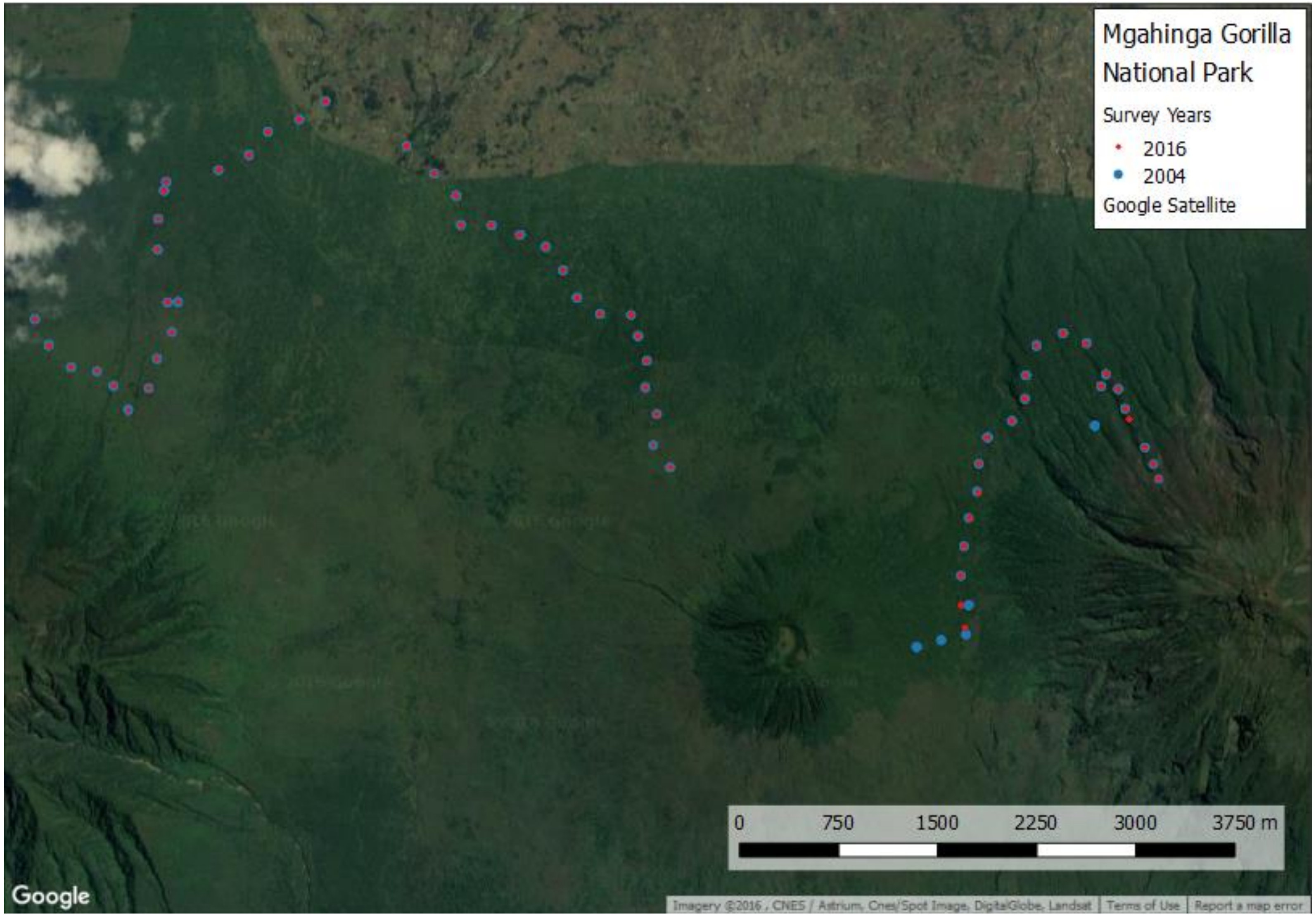


Figure 3.2 Locations of surveys conducted in Mgahinga Gorilla National Park

3.2.2 Predicting species distribution limits

Field survey techniques may have a high number of false absences of species within their range. To account for this, we estimated the probability of species occurrence over the surveyed area using Generalised Additive Models (GAMs) (Wood 2011). GAMs are recommended for this purpose (Meynard and Quinn 2007) as they allow the data to dictate the shape of the curve representing a species probability of occurrence across elevation, rather than assuming a certain relationship *a priori*. This allows for the fitting of non-parametric relationships (Yee and Mitchell 1991). As many Afromontane bird species show seasonal altitudinal movements to lower, warmer altitudes in the cold/wet season (Burgess and Mlingwa 2000, Werema 2015, 2016), we fitted separate GAMs to site occupancy data for each species with 5 or more records in the dataset, with landscape and seasonal information (whether the month was a wet or dry month, and whether it was a hot or cold month) as independent variables.

We classified months into wet or dry and hot or cold months for each landscape depending on whether their mean precipitation was greater or less than the mean precipitation of all months, and hot or cold depending on whether the mean temperate was above or below the mean temperature of the landscape for all months. We determined patterns using precipitation data from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) dataset (Funk et al. 2014) at 0.05° spatial resolution from 2001 to 2016 and temperature data from the Climate Research Unit's (CRU) dataset: CRU TS v3.23 (Harris et al. 2014), at a 0.5° spatial resolution from 2001 to 2014. We only predicted distributions for species with five or more recorded occurrences in the dataset and removed biologically implausible U-shaped responses.

From these predictions, we estimated species' upper and lower range limits setting a limit where the probability of occurrence within a landscape dropped below 1/10th of its maximum occurrence probability for the forest. For lower and upper distribution limits, we compared the earlier and later time periods for both Mgahinga Gorilla National Park and Rwenzori Mountains National Park with Wilcoxon Signed-rank tests.

To determine the rate of climate change occurring in these areas we estimated the change in mean annual temperature experienced by the forests based upon the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) dataset (Funk et al. 2014) at 0.05° spatial. The rate of temperature increase between 1991 and 2014 was used to estimate the warming in each forest between surveys, and this was converted into a predicted change in elevation based on the coefficient of each area's lapse rate, calculated in Chapter 2.

We correlated the values of species functional traits with the elevational distance shifted between survey periods in order to understand the possible causes of variability in rate of distribution change. For each species with estimated range limits we gathered information relating to mass, clutch size, and forest dependency from Birdlife International's Species factsheets (BirdLife International 2016) and the *Handbook of the Birds of the World Alive* (del Hoyo et al. 2016). We recorded forest dependency from Birdlife International's factsheets, as well as mass where possible. These measures of vulnerability to climate change, and of the capacity to mitigate its effects were chosen from other available measures, such as the number of recorded habitat types, because they provided simple, tractable metrics that were available for many species.

When mass data were unavailable from Birdlife International we recorded these data from the Handbook of the Birds of the World Alive along with information relating to clutch size. When we found a range of values or multiple values, we gave preference to values prefaced with "usually" or similar. Otherwise we averaged the range of the values supplied. We found no correlation between mass and clutch size.

We detected range shifts in only 12 species present in Mgahinga Gorilla National Park at either limit, and so could not produce models describing the relationship between functional traits and rate of range shift at that location.

Finally, we conducted successive General Linear Models with backward stepwise elimination of non-significant terms. We modelled upper and lower distribution limits separately. This allowed us to determine what species-specific differences in the degree change in elevation can be explained by mass, clutch size, or forest dependency.

3.3 Results

We compared species distribution limits in earlier and later surveys to identify whether species upper or lower limits had shifted in one direction generally across the community, and to identify the magnitude of that change. We predicted limits for 45 species within Mgahinga Gorilla National Park over the two time-periods, and 60 species at the Rwenzori Mountains National Park. The species-specific limits generated are supplied in the supplementary information. The lower limits of species distributions did not show a significant change across the two time-periods for the whole community in either forest (Figure 3). Species' distributions at Rwenzori Mountains National Park changed significantly at the upper but not the lower limits of species' distributions, showing a median increase of around 400m (Figure 3), but no significant change was seen in the upper limits of species in Mgahinga Gorilla National Park.

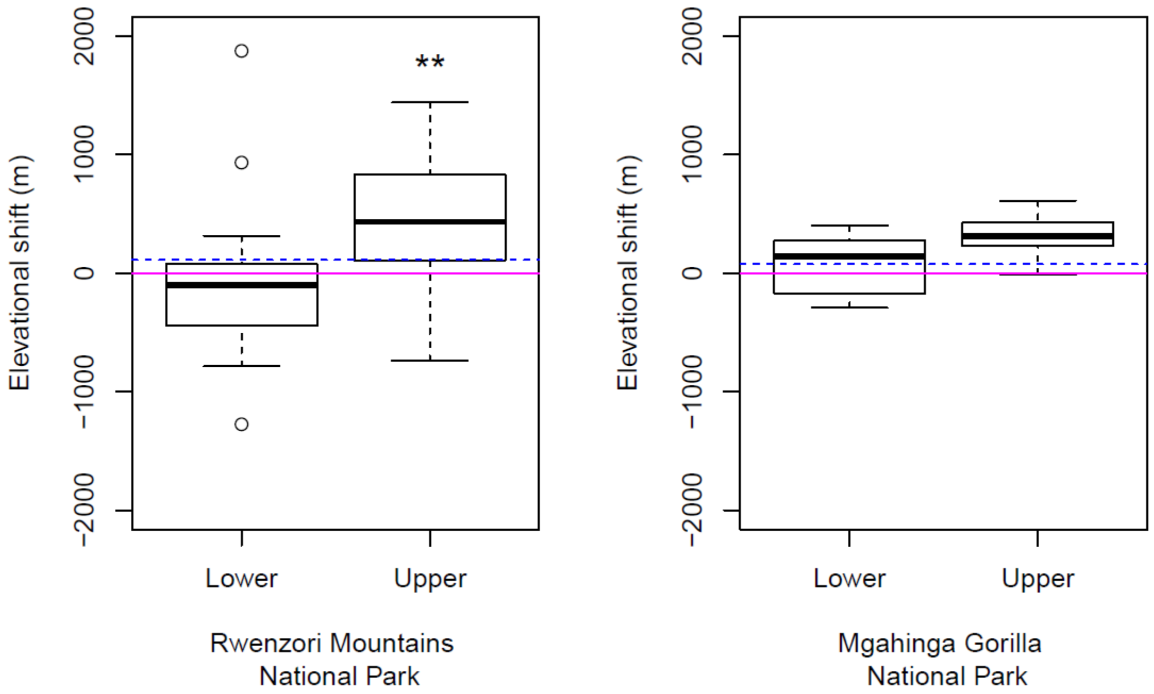


Figure 3.3. Elevational range shifts experienced at species' upper and lower distribution limits between survey periods. Box plots show medians, quartiles, and whiskers at 1.5 the IQR. The solid magenta line marks where no range shift has occurred, whereas the blue dashed line shows the range shift expected if species were to track the estimated temperature change in elevation. "**" indicates that the distribution limit has significantly shifted between sampling periods where $p < 0.005$, in a Wilcoxon signed rank test

We estimated that between 1991 and 2014 Mgahinga Gorilla National Park and the Rwenzori Mountains National Park experienced a respective average of 0.039˚C ($r^2 = 0.36$) and 0.047˚C ($r^2 = 0.361$) warming annually. This would have resulted in a warming of 0.462˚C in Mgahinga Gorilla National Park and 0.652˚C in the Rwenzori Mountains National Park between study periods. Controlling for the lapse rate of their respective locations this warming equates to an expected distance in metres a species would have to move by to exactly track their previous temperatures equal to 76m in Mgahinga Gorilla National Park and 112m in the Rwenzori Mountains National Park. We can compare this to the observed change, a much larger value, to estimate how much of this movement might be accounted for by warming temperatures.

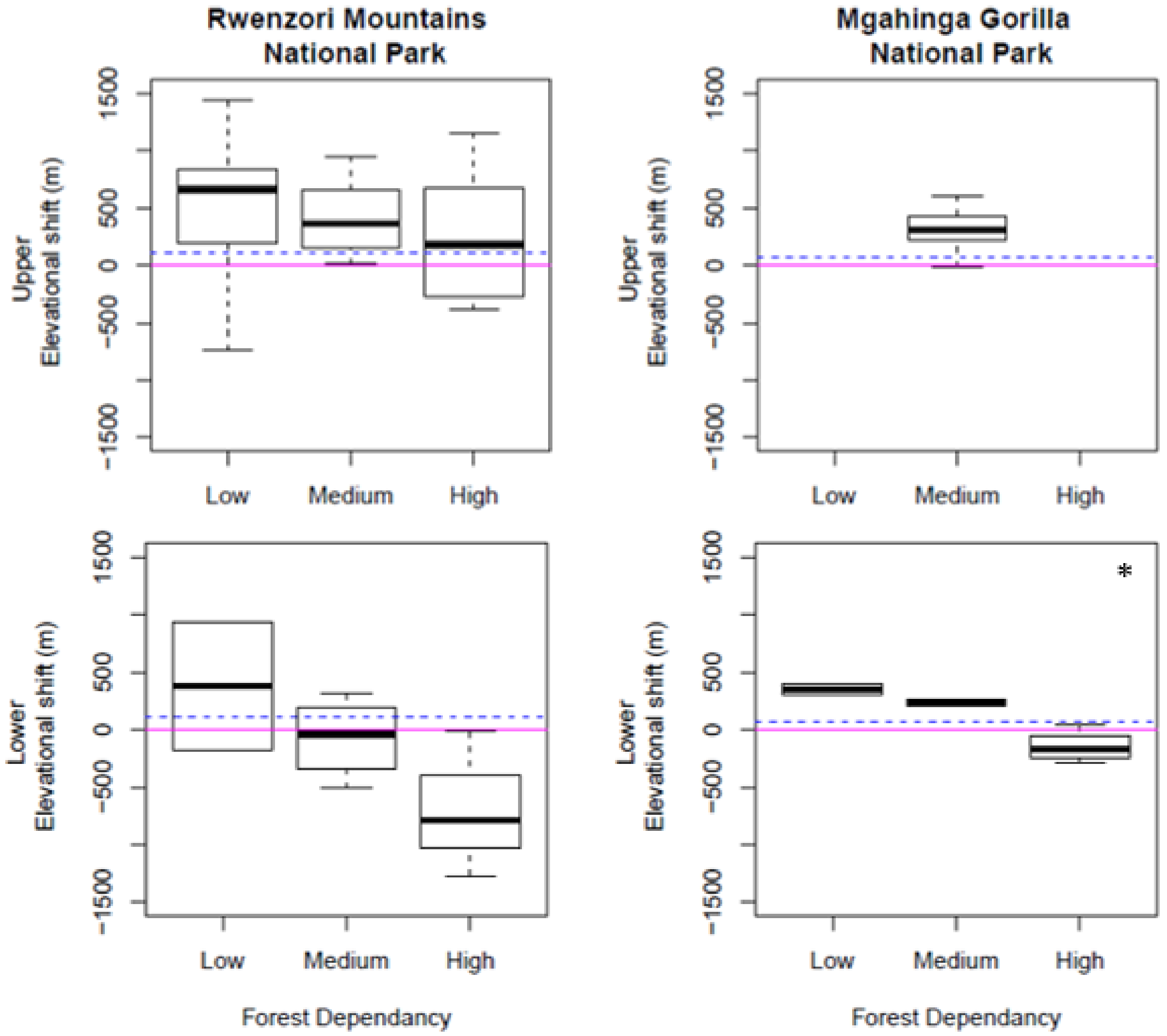


Figure 3.4: Elevational range shifts experienced at species' upper and lower distribution limits between survey periods, separated by the degree of forest dependency. Box plots show medians, quartiles, and whiskers at 1.5 the IQR. The solid magenta line marks where no range shift has occurred, whereas the blue dashed line shows the range shift expected if species were to track the estimated temperature change in elevation.

Of the functional traits examined, only forest dependency was found to significantly correlate with range limits (Table 1), but only at the lower range limits of species in Mgahinga Gorilla National Park. In Mgahinga Gorilla National Park, the lower limits of species negatively correlated with their forest dependency (Figure 4), with negative median range shifts experienced by species with high forest dependency. As only five upper range limits were predicted in Mgahinga Gorilla National Park, and incomplete trait data was available for those species, we were unable to model the relationships of limit elevations to functional trait data (Table 1).

Table 3.1. GLM test statistics and p-values demonstrating that no functional traits examined significantly correlated with limit elevation of upper or lower limits in either forest. We could not conduct GLMs at the upper limits of Mgahinga Gorilla National Park as few species had predicted upper limits there that also had available data for functional traits.

	Rwenzori						Mgahinga					
	Lower			Upper			Lower			Upper		
	DF	F	p	DF	F	p	DF	F	p	DF	F	p
Forest Dependency	2	1.677	0.247	2	0.384	0.687	2	15.465	0.007	NA	NA	NA
Clutch Size	1	4.751	0.054	1	0.001	0.974	1	73.113	0.074	NA	NA	NA
Mass	1	0.567	0.476	1	3.129	0.092	1	0.063	0.814	NA	NA	NA

3.4 Discussion

We rejected our initial hypothesis that at both locations upper and lower limits distributions would have shifted upwards as we only found significant changes for upper distribution limits in the Rwenzori. The only significant change was seen at upper limits, which shifted uphill to a greater extent than lower limits at both sites. The short difference in time between the two survey periods (12 years between surveys at Mgahinga Gorilla National Park and 14 years between surveys at Rwenzori Mountains National Park) may mean that changes in temperature have not been great enough to result in shifts at most limits: indeed, we estimated that the distance required for shifts to track climate change were much smaller than those observed. As has been demonstrated for many species, our populations may still be reacting to changes in climate (Dullinger et al. 2012, Halley et al. 2016), and the observed change in elevation may be small compared to the annual variation observed that occurs in these species. Our work examines the change of species distributions in just over a decade of change, many studies have examined longer periods of change (Chen et al. 2009, Felde et al. 2012, Auer and King 2014), but shorter studies have found significant upwards shifts. The large change observed indicates that factors other than temperature may have been partially responsible for the observed differences in altitude between the two time periods, and it would be useful for future studies to examine the role that seasonal movement has to play in determining the limits of the species examined.

An important caveat of the study is that we could not compare species distributions within the same season. The seasonal movement of birds is a recognised phenomenon where birds move downhill in the wet, cold season (Burgess and Mlingwa 2000); we included season as an argument in the distribution GAMs because of their importance and we accounted for its effect by averaging the resulting predictions. Due to low data availability across seasons, we employed this method rather than comparing results from different time periods within season. Consequently, we could not fully account for the importance of seasonal movement. The distance moved in such seasonal migrations is not well known. Surveys conducted in Mgahinga Gorilla National Park were all in the cold seasons, mostly in the wet cold season, so changes observed there are unlikely to be caused by seasonal movement. However, surveys within Rwenzori Mountains National Park were conducted in the dry season in the earlier sampling period (mostly the cold, dry season) and the wet season in the later sampling period (mostly the hot, wet season), which might be expected to result in upwards shifts in distribution. This work highlights the importance of accounting for seasonality in work on distribution limits. Being unable to do so in this study may have obfuscated trends in the data and limited our confidence in observed relationships. As such we should be especially cautious in interpreting these results. Furthermore, previous work has highlighted that the most abundant species, those best represented in the data, may be disproportionately likely to be habitat generalists and as such it is possible that we have been biased towards describing species that are least likely to experience barriers blocking their movement uphill (Thomas 2010). However, our shifting species represented all levels of forest dependency and we believe our results are applicable to habitat generalists and specialists alike.

The complicated picture of lower-limit range shifts in this analysis is not wholly unexpected. Numerous stressors are acting on species within the community that may work to balance or reverse the effects of rising temperatures. For example, we are aware that the complicated way in which climate change may affect precipitation can result in range shifts in unexpected directions (Thomas 2010, VanDerWal et al. 2013). As detailed rainfall data was unavailable, especially across the elevational range considered, we could not account for changes to precipitation that may have occurred. We are also aware that since the gazetting of the parks in 1991, the low elevation forest quality has been continually improving as it regenerates from farming to tropical forest. This improved habitat quality may have meant that, despite warming, the low elevations of the national parks may have become more suitable since the early 2000s and is supported by the significant, negative relationship observed between species' lower range limit elevation at Mgahinga Gorilla National Park and their degree of forest dependency. As such the diversity of estimated range shifts may be partially explained by rainfall or habitat change. It must be noted that the lowest survey altitude at Mgahinga Gorilla National park was conducted at over 2300m, higher than the average lower elevational limits of species predicted in the previous chapter (around 2200m); this indicates that many species may be comfortably within their temperature niche. Surveys at Rwenzori Mountains National Park begin from around 1800m allowing for the lower limits of many species to be present within the elevational range of the data.

Although different directions of change were observed at upper and lower distribution limits within the Rwenzori Mountains National Park, we are confident in our conclusions concerning range changes at the upper limits. As shown in the previous chapter, the determining factors for upper and lower range limits may be different and so we should not expect changes at both range limits to closely align in all cases. However, range changes at the lower limits of distributions within this park were not significant and we must be cautious in interpreting those results. As we could only estimate the change in upper range limit for 5 species at Mgahinga Gorilla National Park it would not have been possible to observe significant changes; but qualitatively, we observed a general uphill shift of upper range limits of a similar magnitude at both parks despite covering different time periods. The low statistical power of the analysis of the Mgahinga Gorilla National Park data at both upper and lower limit means that we cannot draw firm conclusions concerning range changes there.

Qualitatively the size of the effect is similar for both regions, although they consider different time periods. In both cases the median species range shift was larger than expected from tracking temperature changes alone. Lower limits may be expanding downhill in the Rwenzori Mountains National Park and although the change is not significant there could be several causes of downhill expansion. For example, an increase in abundance might cause a species to expand in distribution at both upper and lower limits (Brown 1984), though this reason seems unlikely to account for a general downwards trend across all species. The larger change observed at upper limits when compared to lower limits is not unexpected, occurring in previous work (Bergamini et al. 2009, Menendez et al. 2014) and partially explained by factors such as the asymmetry present in relative ease of a single individual colonising new areas in range expansion and the loss of every individual in an area needed for range contraction. Alternatively, the lower limits of species distributions may have been less likely to shift uphill tracking temperature change due to differences in how temperature controls upper and lower limits. For example, lower limits may be more sensitive to extremes of high temperature, or mountain lowlands in this area may form favourable microclimates that shelter species from the effect of temperature change.

To understand the observed changes in distributions, we modelled the effects of three functional traits: mass, clutch size, and forest dependency. Mass and clutch size have been highlighted as traits indicating risk from climate change (Foden et al. 2013, Trivino et al. 2013) and forest dependence has been selected as a measure of habitat specificity which can influence the ability of species to find suitable habitat within their new range (Foden et al. 2013). As only forest dependency displayed a significant relationship with magnitude of range shifts, and then only at low elevation limits in one park, we agree with previous work (Angert et al. 2011) in advising that function trait data may be of limited predictive value in assessing the likelihood of species experiencing range shifts. However, we suggest that our results are interpreted carefully as they are based upon a small number of species. Furthermore, the low statistical power of our observations has prevented us from incorporating phylogeny as would be ideal in studies of this kind (Angert et al. 2011). We are unable to explain the direction or rate of change at the upper distribution limits of species in the Rwenzori Mountains National Park using the functional trails examined, despite their significant uphill shift.

Our work indicates that upward shifts appear to have already occurred in the avifaunal communities of these two Ugandan National Parks, but are perhaps confounded by seasonal movements of species. In agreement with previous work (Hickling et al. 2006, Raxworthy et al. 2008, Chen et al. 2011), we observed larger range limit shifts at the upper range limits of species distributions than predicted by populations tacking observed warming directly. As we have been unable to account for the seasonal effect of movement on these populations (Burgess and Mlingwa 2000) and giver the low statistical power of these results, we should be cautious in interpreting them. However, these results seem broadly consistent with range shifts observed in other warming environments. If these results are indicative of changes generally experienced in the Albertine Rift ecoregion, in which these national parks are situated, widespread shifts in range may be occurring. As species shift their distributions, the spatial availability of natural resources and the provisioning of services may change too, impacting stakeholders (Carr et al. 2013).

Chapter 4: Key Finding and Discussion

4.1 Key Findings

The preceding chapters closely examined two aspects of the study of avian range limits in Afromontane communities. I increased understanding of the role of biotic interactions in determining upper and lower range limits across an elevational stress gradient; and I have summarised how species' distributions appear to have shifted in elevation in two well studied Ugandan national parks. I identified these areas as recognised knowledge gaps in the study of species' distribution limits in my introduction and in addressing them I have employed novel methods and introduced new data.

Initially, I identified a long-established assumption in ecological work that low stress distribution limits, often warm limits, were more likely to have biotic proximate causes than their high stress counterparts, cold limits (MacArthur and Wilson 1967). This assumption is prevalent, but has yet to be effectively corroborated by large-scale studies or reviews (Normand et al. 2009, Jankowski et al. 2010, Wiens 2011, Wisz et al. 2013, Cahill et al. 2014). I set out to provide a large-scale study that might support or weaken the case for this assumption by identifying the fingerprint of biotic interactions on warm, low elevation range limits of numerous avifaunal species across a large geographic range. I predicted that generally across multiple Afromontane communities, a species' cold limits would vary little, whereas warm limits would vary across communities in correlation with the species richness of the community.

Unexpectedly, I found species' cold range limits to be highly variable in elevation across different communities, more variable than species' warm range limits. This effect was lessened but persisted when accounting for the effect of differing lapse rates across mountain ecosystems. We assert that this result reflects a genuine biological pattern, rather than a methodological artefact as limits were not set lower in communities on smaller mountains because data at higher elevations was unavailable, but because populations were estimated to decline in abundance at a lower elevation on smaller mountains. Data were not extrapolated, all limits occur within the surveyed elevational range of the relevant landscape. As such it seems unlikely that this effect is a result of limitations in data availability, collection, or analysis. When determining the relationship between limit variability and various landscape properties, the greater variability of upper limits was partially explained by lapse rate and the upper bound of forest cover for the landscape. However, I observed a strong relationship between the elevation of cold limits and the maximum elevation surveyed in the area, indicating that mountain height may have a strong role to play in determining where elevational limits are set, both for cold and warm distribution limits.

As far as I am aware, no work has looked directly at the variability of species' range limits across an environmental stress gradient in relation to the importance of biotic processes in determining range limits. Although range limit variability has been studied in the context of seasonal effects (Sheldon et al. 2015) and in examining how climate change may affect abundance at range margins (Oliver et al. 2012). As such I believe this observation of increased variability in upper distribution limits on mountains is new. I believe that the effect of maximum survey elevation, thought to be linked to mountain height, is likely to be indirect as most species' cold limits are not located near either the elevational peaks of their montane communities or the upper limits of forest cover. As the mechanism of this relationship is indeterminate, it is important to consider why this result may occur. One explanation for this may be that as warming occurs on large mountains species are able shift to colder elevations without impediment. However, on smaller mountains where cold limits may be very close in elevation to the height of the mountain, the highest species may be unable to shift upwards. These small populations would face strong selective pressure to adapt to warmer conditions and conserve or even expand their warm limits. As the species is squeezed, species from lower elevations expanding upwards would face increased competition (Jankowski et al. 2010) which may lead to squeezing continuing to additional species, upper limits may occur lower down on lower mountains. We might expect populations to adapt to become competitive at their warm limits as has been shown to occur in some montane species (Gifford and Kozak 2012). This is supported by the observation of stronger relationships between species richness and limit elevation at warm limits than at cold ones, with a negative direction at warm limits and a positive direction at cold limits. In addition, this tentatively supports the main assumption tested, that the importance of biotic interactions in setting range limits is greater at warm limits. Species-rich landscapes generally contained populations with broader distributions than landscapes with low species richness and it is not entirely clear why. There may be a relationship between species richness and habitat quality which may also drive abundance (Brown 1984). Further work would be needed to establish the cause of this relationship as many landscape factors and the stochastic elements of colonisation and extinction may influence species richness (Weiher et al. 2011). Unfortunately, I was unable to assess the importance of precipitation in determining range limits, as high quality, high resolution data were unavailable for the region, especially for locally validated data across an elevational gradient. This black box of precipitation is extremely difficult to assess without better planning and investment in monitoring in the national parks of the Albertine Rift. Indeed, the problem is not unique to the region, with many parts of Africa lacking rainfall gauge data, and further development and planning in Africa has been called for to address this (Hughes 2006a, b, Dutra et al. 2013).

In my second chapter I responded to further concerns raised in the introduction, that highlighted how previous work has yet to comprehensively describe species distribution and range shift trends in the montane tropics (Thomas 2010, Cahill et al. 2014). Despite exemplary work documenting range shifts of large numbers of species in Borneo (Chen et al. 2009), Australia (Williams et al. 2003, Staunton et al. 2016), and Madagascar (Raxworthy et al. 2008), much work must be done to document range shifts in the many other understudied environments found in tropical montane systems. As there are good theoretical reasons to believe that biotic interactions are stronger at the tropics, as demonstrated for predation (Freestone et al. 2011), biotic resistance (Freestone et al. 2013), and other interactions (Schemske et al. 2009), there is a need to improve our understanding of tropical range limits.

My second data chapter brings attention to apparent uphill changes to avifaunal distribution limits that have been significant for high altitude limits at the Rwenzori Mountains National Park, but may also be occurring elsewhere in the region. We cannot separate out a possible confounding effect caused by seasonal movement and future studies should try to control for this. These results generally agree with previous studies showing rapid range shifts in response to climate change (Hickling et al. 2006, Chen et al. 2011). However, there were also non-significant indications of downhill shifts in elevation at the lower limits of distributions within Rwenzori Mountains National Park. High forest dependency was associated with downhill range shifts at lower limits, which supports an explanation that improving habitat quality may have facilitated this, following the gazetting of the national parks in 1991. Why species might be shifting ranges to colder environments at a rate faster than expected is not fully understood; we suggest that this may be occurring in avifaunal populations in Ugandan Afromontane forest, requiring further investigation.

For both upper and lower limits, we correlated the rate of range limit change experienced by each species with three functional traits: mass, clutch size, and forest dependency. These are thought to generally reflect the sensitivity and adaptive capacity of species to change in related studies (Foden et al. 2013, Trivino et al. 2013), but were not found to correlate with the changes in elevation seen at either cold or warm limits of species' distributions at either location. Issues of statistical power remained due to the low number of species included in the analysis. The elevation of the low elevation distribution limits appeared to be negatively associated with a species' forest dependence; with highly dependent species having a greater, but non-significant, downhill shift over time. As noted above, this may reflect the continually improving quality of lower elevation forest since the park's gazetting.

There remains a need to conduct repeat surveys of previously visited study locations in order to assess how changing climate is affecting species distributions; the ecological monitoring network in Africa is less developed and effective than that of any other continent with internal ecological monitoring (Yevide et al. 2016). Only a small fraction of my dataset was collected in a way that allowed me to assess how warming may affect species distribution limits in the Albertine Rift across the duration of the study. With a larger number of communities and additional functional trait measures relating to risk from climate change a better understanding of the rapid range shifts observed may have been reached, as in Auer and King (2014). Additionally, if more communities were analysed a cross community analysis, examining species richness, vegetation cover, or lapse rate, might increase my understanding of the proximate causes of range limit shifts, as I did in the first chapter. But while lacking the appropriate data I cannot comment on the importance of those abiotic factors.

Taken together the two chapters of this work make progress towards a fuller understanding of the importance of biotic and abiotic factors in limiting the distributions of Afromontane avifauna. The difference observed between warm and cold limits shows the importance of separately examining each range limit. By doing so I have built understanding of the relative importance of different factors in determining where the boundaries of species distributions are set and both chapters have identified new questions. I have added to a growing body of work that suggests classical assumptions about the importance of biotic interactions in limiting species distributions may be overstated (Cahill et al. 2014). However, my findings indicate that biotic interactions may have a greater effect at warm limits than at cold limits. This agrees with a weaker version of this theory that states that the relative importance of biotic interactions is greater at low stress limits than high stress limits, despite abiotic factors being the predominant limitation of both high and low stress range boundaries. I have highlighted possible range shifts that appear to be occurring faster than expected from climate change alone. Existing literature has already called for more data to investigate this trend (Chen et al. 2011). Factors other than temperature appear to be involved in these range shifts, and this may be supported by the first chapter, where temperature was not found to be the most important determinant of limit variability. Forest dependency is significantly negatively correlated with lower distribution limits at Mgahinga Gorilla National Park. Following my finding from the first chapter showing a positive relationship between the upper limits of forest cover and cold limits of a species distribution, I cautiously expect increasing forest cover to partially explain this change, however I was unable to ascertain the change in forested area at the tops of these mountains during this period. Although treelines around the world are experiencing change, the sessile nature of plants and the slow reproductive cycles of trees leads us to expect that rapid avian shifts are unlikely to be mediated by habitat, indeed, a review of treeline studies (though mostly temperate) found only half reported treeline's to have changed since 1900 (Harsch et al. 2009). Changes to forest composition and elevation appear to be slow, perhaps too slow to detect at the landscape level in many cases (Gottfried et al. 2012). Unfortunately, I was not able to determine the proximate causes of either the range limit variability, or the range shifts; although I have been able to suggest areas for future research and have highlighted an important knowledge gap: why are upper limits so variable across mountain communities?

4.2 Challenges and considerations when generalising results

A number of challenges were faced in interpreting the data. Studies that use large, biodiverse datasets, covering broad geographic areas and multiple communities (Kissling et al. 2012, Wisz et al. 2013, Mouquet et al. 2015) are likely to encounter large numbers of species with few species records. Excluding species from these datasets risks ignoring the broader trends experienced by the whole community, not just abundant or generalist species. I included these species, though there are concerns surrounding this approach. The low number of records for these species might be resolved by additional surveys within an area. This has clear logistical and financial costs, and would require careful planning to ensure new study transects were not simply pseudo-replicates containing the same individuals but recorded from another location. This challenge is a persistent one for studies of species existing at a low density compared to the size of the study area (Beale and Lennon 2012): the mountain transects, or species that are difficult to identify in visual and audial surveys because of their behaviour.

I have also provided an example of apparent range shifts occurring in the upper limits of species in the Rwenzori Mountains National Park, and indications that the same may be occurring at Mgahinga Gorilla National Park. While doing so I have been working with a large dataset, covering a broad geographic range, multiple communities and a large number of species, as has been called for in much of the literature records (Araujo and Guisan 2006, Kissling et al. 2012, Wisz et al. 2013, Mouquet et al. 2015, Singer et al. 2016). However, I was not able to meet all recommendations; notably, I was unable to identify the proximate causes that limited distributions, as has been recommended (Cahill et al. 2014), and instead only determined the correlations of limits with independent variables, such as temperature and species richness. Identifying these proximate causes would be difficult due to the large number of species and the sparsity of many species records, making the data much more useful for examining across-community trends rather than species specific responses. I included other recommendations of Cahill (2014), such as analysing upper and warm range limits separately. Any challenges in examining data of this kind may be common to other similar, yet valuable, datasets gathered on such a large scale. I have demonstrated that despite challenging decisions to be made during the analysis of such data, valuable and interesting conclusions can be gained from large scale datasets if the inherent benefits and strengths of such data are utilised.

Further work should also be conducted revisiting additional previously surveyed sites, as we did with sites for the second chapter of this work. Repeat surveys of this nature will allow us to compare across ecosystems to determine how abiotic factors affect range shifts in the region. However, improving our understanding of the variability of species' range limits across similar communities is now a clear goal for future studies of species' distributions, with most previous work on range limit variability looking at variability due to seasonal effects or change over time (Giesecke et al. 2010, Sheldon et al. 2015), with some studies predicting and finding range limits to be more variable in abundance over time (Oliver et al. 2012). However, I am not aware of any studies looking at the variability of species range limits spatially, in a way that relates that variability to biotic and abiotic processes. Examining limit variability enables the formation of testable predictions that utilise large scale, multi-species datasets, which should be welcomed. Repeating the work conducted here in more fully documented tropical montane communities, for which detailed temperature, precipitation, lapse rate, and vegetation cover data can be acquired, would be an obvious step forward. New hypotheses about how abiotic and biotic factors might alter the variability of upper range limits are required and this under-utilised method of examining range limits deserves greater exploration. More direct measures of biotic interaction strength could be used, rather than using species richness. Species richness is only a proxy for the degree to which species exert biotic pressure on one another. Increased richness may have an antagonistic, cooperative, or neutral impact of any given species and generalising the effect of increased richness across a community, as must be done when studying many species, is difficult. More direct measures of biotic interaction might include direct measures of predation rates (Schemske et al. 2009), specific mutualisms (Schemske et al. 2009), disease or parasitism, behaviours relating to aggression (Freeman 2016), and other indices directly relating to interactions; however, it is often difficult to interpret. Synthesising these results into an interaction matrix and determining the connectivity of these communities may reach a description of biotic interaction strength closer to reality than any individual measure and it may be possible to construct such measures from spatial data using machine learning methods (Faisal et al. 2010). If my suggestion, that increased competitiveness at warm limits on smaller mountains is resulting in increased variability of upper limits across communities, we should expect to observe increased competition, aggression, or other biotic interactions that reinforce the warm boundary of species' distribution limits. A study that compared the strength of various biotic interactions at range limits on different landscapes of the Afromontane forests, using established methods, such as noting aggressive behaviours in response to playbacks of bird calls, could test this hypothesis and has been described in more detail above.

4.3 Conclusions

In summary, my thesis addresses knowledge gaps and calls for range limit studies existing in the literature. In the two preceding data chapters I have added to existing knowledge on these topics and identified new questions of interest to the field. My results have been analysed in the context of existing work on the topic. Though I have not been able to cover all recommendations highlighted in the literature review, my analyses are informed by and firmly grounded in previous research. Areas of research have been highlighted for future work as well as suggestions for specific experiments. My results suggest that species distribution limits are complex in nature, explained by both biotic and abiotic factors and supports findings that incorporating biotic interactions is important in species distribution models (Kissling et al. 2012, de Araujo et al. 2014). The processes that determine limits may differ at high and low stress limits and the consequences of this on modelling distributions should be further investigated. The study of range limits remains a topic of great interest in ecological research, and perhaps the most intriguing finding of the work was that so much is left to know concerning the variability of limits across different communities. Undoubtedly, investigations into the topic will require similarly large datasets to be collected, fulfilling calls for datasets with a broad geographic coverage of multiple species. Such work may benefit from considering mountain height and the possible indirect effect of mountain size on determining limits, as has been suggested in this work.

Appendices

Appendix 1: Landscape Variables

Table 5.1 The lapse rates of the Landscapes of the Albertine Rift (°C 100m-1)

Lapse Rate (˚C 100m^-1)	Murchison - Semliki	Kahuzi Biega	Itwombwe Balala	Kabobo-Marungu	Greater Mahale System	Queen Elizabeth	Ruwenzori	North Kivu	Virunga	Congo-Nile Divide
DRY COLD	NA	-0.521	-0.594	-0.651	-0.914	-0.83	-0.573	-0.585	-0.61	-0.64
DRY HOT	-0.808	-0.594	-0.64	-0.611	-0.742	-0.936	-0.574	-0.583	-0.613	-0.725
WET COLD	-0.807	-0.654	-0.64	-0.598	-0.901	-0.882	-0.575	-0.717	-0.578	-0.686
WET HOT	-0.806	-0.6	-0.652	-0.658	-0.887	-0.88	-0.602	-0.637	-0.641	-0.73

Table 5.2. The observed species richness, predicted species pool size with standard errors and number of sites in the sample.

Landscape	**Observed species**	**Species pool - Chao**	**s.e.**	**Number of sites**	**Lower forest limit**	**Upper forest limit**	**Forest extent**	**Min survey alt**	**Max survey alt**	**Survey Range**
Murchison-Semliki	317	375.81	19.02	1079	623	1532	909	613	1279	666
Kahuzi Biega	148	163.09	8.41	475	519	3100	2581	1062	2732	1670
Itwombwe-Balala	128	180.45	27.85	463	584	3219	2635	936	2650	1714
Kabobo - Marungu	130	169.93	19.46	374	647	2637	1990	889	2691	1802
Greater Mahale System	133	173	17.24	371	786	2420	1635	771	2454	1683
Queen Elizabeth	271	330.68	18.71	752	920	1830	910	665	1633	968
Ruwenzori	297	383.27	28.58	1434	665	3170	2505	624	4520	3896
North Kivu	109	135.6	12.34	77	596	2305	1709	1069	2024	955
Virunga	244	269.33	10.61	1091	954	2293	1340	1337	3834	2497
Congo-Nile Divide	127	147.03	12.21	781	1453	2886	1432	1675	2834	1159

Appendix 2: Species movement rates and trait data

Table 6.1: Limit and functional trait information for species in Mgahinga Gorilla National Park and Rwenzori Mountains National Park

	Lower Limits				Upper Limits				Red list	Forest Dependency	Mass	clutch size	Artificial/Terrestrial: Gardens farmland plantation	Artificial/Terrestrial: Degraded Forest	Desert	Urban	Forest	Grassland	Marine	Rocky Areas	Savanna	Scrubland	Wetlands	Altitude	Agriculture	Logging	Habitat Shifting and alteration
	Rwenzori		Mgahinga		Rwenzori		Mgahinga																				
Species	Before	After	Before	After	Before	After	Before	After																			
Andropadus latirostris	NA	NA	NA	NA	2312	2472	2821	2810	LC	Medium	29	2	1	1	0	0	1	0	0	0	1	1	0	NA	0	0	0
Andropadus virens	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	27	2	1	1	0	0	1	0	0	0	1	1	0	0 - 2200	0	0	0
Apalis personata	3095	NA	2685	NA	3026	3136	3018	NA	LC	Medium	5	NA	0	1	0	0	1	0	0	0	0	0	0	1270 - 2800	0	0	0
Apalis porphyrolaema	NA	2084	2561	2355	2623	3192	3136	NA	LC	High	54	NA	0	0	0	0	1	0	0	0	0	0	0	1600 - 3400	0	0	0
Arizelocichla nigriceps kikuyuensis	2216	1974	2631	NA	3136	3510	2753	NA	LC	Medium	34	2	0	1	0	0	1	0	0	0	0	1	0	700 - 3300	0	0	0
Bathmocercus rufus	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	17	2	0	0	0	0	1	0	0	0	0	0	0	NA	0	0	0
Batis diops	2642	NA	2975	3217	2889	3247	2857	3086	LC	Medium	10	NA	0	0	0	0	1	0	0	0	0	1	0	1340 - 3300	0	0	0
Batis molitor	NA	NA	NA	NA	NA	2915	NA	2475	LC	Low	1	2	0	0	0	0	1	1	0	0	1	1	0	NA	0	0	0
Bradypterus cinnamomeus	2202	2029	NA	2846	3081	4520	NA	NA	LC	Low	21	2 5	0	0	0	0	1	0	0	0	0	1	0	1300 - 3300	0	0	0
Buteo oreophilus	NA	2472	NA	2696	NA	NA	NA	NA	NT	High	46	2	0	0	0	0	1	1	0	0	0	0	0	2000 - 3800	1	1	0
Cercococcyx olivinus	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	43	NA	0	1	0	0	1	0	0	0	0	0	0	NA	0	0	0
Chloropeta similis	NA	2001	NA	3121	3429	3621	3415	NA	LC	Low	7	2	0	0	0	0	1	0	0	0	0	1	1	1800 - 3700	0	0	0
Chrysococcyx cupreus	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	35	NA	0	0	0	0	1	0	0	0	1	1	0	0 - 3000	0	0	0

Chrysococcyx klaas	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	28	NA	0	0	0	0	1	0	0	0	1	1	0	0 - 3000	0	0	0
Cinnyricinclus sharpii	NA	NA	NA	NA	NA	NA	NA	NA	LC	High	40	3	0	0	0	0	1	0	0	0	0	0	0	1800 - 2500	0	0	0
Cinnyris chloropygia	NA	NA	NA	NA	NA	2195	NA	2642	LC	Medium	42	2	1	0	0	1	1	0	0	0	1	1	0	NA	0	0	0
Cinnyris regia	2037	2112	NA	2822	3457	3468	2878	NA	LC	Medium	44	1	0	0	0	0	1	0	0	0	0	1	0	1500 - 3100	0	0	0
Cinnyris reichenowi	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	50	1 5	1	0	0	0	1	1	0	0	1	1	0	NA	0	0	0
Cinnyris stuhlmanni	NA	2084	2588	2990	2825	3662	NA	NA	LC	Low	54	1	1	0	0	0	1	1	0	0	1	1	0	NA	0	0	1
Cinnyris venusta	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	50	2	1	1	0	0	1	1	0	0	1	1	1	NA	0	0	0
Cisticola chubbi	3493	NA	3361	NA	3072	2334	2996	NA	LC	Low	15	2 5	1	0	0	0	1	1	0	0	0	1	1	1200 - 3350	0	0	0
Columba arquatrix	3109	2666	2685	NA	2971	3925	3000	3313	LC	Medium	33	1	1	0	0	0	1	0	0	0	0	0	0	300 - 3200	0	0	0
Corvus albicollis	NA	3634	NA	NA	NA	3911	NA	NA	LC	Low	53	4	1	0	0	1	1	1	0	1	1	0	1	1000 - 3000	0	0	0
Cossypha archeri	2578	NA	2900	2942	3274	4437	3071	NA	LC	High	23	2	0	0	0	0	1	0	0	0	0	1	0	1660 - 4300	0	0	0
Cryptospiza jacksoni	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	13	2	0	0	0	0	1	0	0	0	0	1	0	1550 - 3200	0	0	0
Cuculus solitarius	2793	2693	NA	NA	NA	2610	2560	2984	LC	Medium	48	NA	0	0	0	0	1	0	0	0	1	1	0	1000 - 3000	0	0	0
Cyanomitra alinae	NA	NA	3088	NA	3411	NA	2803	NA	LC	High	11	1 5	0	0	0	0	1	0	0	0	0	0	0	1400 - 3280	0	0	0
Cyanomitra olivacea	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	45	2	1	0	0	0	1	0	0	0	0	1	0	NA	0	0	0
Dendropicos griseocephalus	NA	3122	NA	2858	NA	3330	NA	3032	LC	Medium	37	2 5	0	0	0	0	1	0	0	0	0	1	1	450 - 3700	0	0	0
Dryoscopus gambensis	NA	NA	NA	NA	NA	2167	NA	3109	LC	Low	31	2 5	1	1	0	0	1	1	0	0	1	0	0	NA	0	0	0
Illadopsis pyrrhoptera	NA	NA	NA	NA	NA	NA	NA	NA	LC	High	26	2	0	0	0	0	1	0	0	0	0	0	0	1550 - 2800	0	0	0
Laniarius luehderi	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	38	1 5	1	1	0	0	1	0	0	0	0	1	0	NA	0	0	0
Laniarius poensis	1982	2001	NA	NA	3063	3717	2502	NA	LC	Medium	39	2	0	0	0	0	1	0	0	0	0	0	0	0 - 3000	0	0	0
Malaconotus dohertyi	2353	NA	2406	NA	2898	NA	2964	NA	LC	Low	36	NA	1	0	0	0	1	0	0	0	0	1	0	1500 - 3350	0	0	0
Milvus migrans	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	52	2 5	1	0	1	1	1	1	1	0	1	1	1	0 - 4900	0	0	0
Muscicapa adusta	NA	NA	NA	NA	NA	2417	NA	2295	LC	Low	2	3	1	0	0	1	1	0	0	0	1	1	0	0 - 3400	0	0	0
Nectarinia johnstoni	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	15	1	0	0	0	0	1	1	NA	0	0	1	0	1900 - 4400	0	0	0

Nectarinia purpureiventris	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	8	1 5	0	0	0	0	1	0	0	0	0	0	0	NA	0	0	0
Onychognathus tenuirostris	NA	NA	NA	NA	NA	NA	NA	NA	LC	High	12	3	0	0	0	0	1	1	0	1	0	0	1	1200 - 4250	0	0	0
Oreolais ruwenzori	2175	NA	2540	2774	2683	3524	3147	NA	LC	Medium	56	2	0	1	0	0	1	0	0	0	0	1	0	1550 - 3100	0	0	0
Parus fasciiventer	3576	2306	3388	3098	3924	3648	NA	NA	LC	High	14	1 62	0	0	0	0	1	0	0	0	0	0	0	1800 - 3400	0	0	0
Phyllastrephus flavostriatus	NA	2984	NA	2678	NA	3247	NA	2942	LC	Medium	32	2	0	0	0	0	1	0	0	0	0	1	0	0 - 3000	0	0	0
Phylloscopus laetus	2953	2167	2551	NA	3741	3358	2810	NA	LC	High	1	2 5	0	0	0	0	1	0	0	0	0	0	0	1200 - 3100	0	0	0
Phylloscopus umbrovirens	2587	2901	NA	3241	NA	4133	2626	NA	LC	Medium	1	2 5	0	0	0	0	1	0	0	0	0	1	0	1500 - 4300	0	0	0
Ploceus alienus	NA	3496	NA	2666	NA	3607	NA	3038	LC	Medium	22	2	0	0	0	0	1	0	0	0	0	0	0	1500 - 2700	0	0	0
Pogoniulus bilineatus	2532	4409	2599	NA	2477	2693	2631	3241	LC	Medium	9	3	1	0	0	0	1	0	0	0	1	1	1	0 - 3000	0	0	0
Pogoniulus coryphaeus	2889	NA	2352	NA	2958	NA	2753	NA	LC	Medium	3	3	1	0	0	0	1	0	0	0	1	1	0	900 - 3030	0	0	0
Pogonocichla stellata	2651	2140	2574	NA	3864	4520	2642	NA	LC	Medium	19	2	1	0	0	0	1	0	0	0	0	1	0	1600 - 4300	0	0	0
Prinia bairdii	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	11	3	NA	1	0	0	1	0	0	0	0	1	0	1500 - 3000	0	0	0
Psalidoprocne pristoptera	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	6	2	1	1	0	1	1	1	0	0	1	1	1	300 - 2400	0	0	0
Pseudoalcippe abyssinica	3260	NA	NA	NA	2971	2763	2735	NA	LC	High	20	2	1	0	0	0	1	0	0	0	0	1	0	900 - 3000	0	0	0
Pycnonotus barbatus	2532	3468	NA	NA	2147	2638	2703	NA	LC	Low	30	3 5	1	0	1	0	1	0	0	0	1	1	1	0 - 3000	0	0	0
Serinus gularis	2367	NA	NA	NA	NA	NA	2531	NA	LC	Low	15	3	1	0	0	0	1	0	0	0	1	1	0	0 - 2100	0	0	0
Serinus striolatus	NA	2998	NA	NA	NA	NA	NA	2666	LC	Low	18	4 5	1	0	0	0	1	0	0	0	0	1	0	1300 - 4300	0	0	0
Streptopelia semitorquata	NA	NA	NA	NA	1872	NA	2583	NA	LC	Medium	16	2	1	0	0	1	1	0	0	0	1	1	1	200 - 2100	0	0	0
Sylvietta leocophrys	NA	NA	NA	NA	NA	NA	NA	NA	LC	Medium	51	2	0	0	0	0	1	0	0	0	0	1	0	1290 - 2500	0	0	0
Tachymarptis melba	NA	NA	NA	NA	NA	NA	NA	NA	LC	Low	49	3	0	0	0	1	1	1	0	1	1	1	1	0 - 2800	0	0	0
Tauraco johnstoni	2655	2638	2669	2534	3411	4091	2352	NA	LC	High	25	1 5	0	0	0	0	1	0	0	0	0	0	0	2000 - 3600	0	0	0
Tauraco schuetti	NA	NA	NA	NA	NA	3579	NA	3109	LC	High	24	2	0	0	0	0	1	0	0	0	0	0	0	500 - 2800	0	0	0
Trochocercus albonotatus	NA	3150	NA	2720	NA	3385	NA	2978	LC	Medium	55	2	0	0	0	0	1	0	0	0	0	1	0	350 - 2700	0	0	0
Turdus olivaceus	NA	2278	NA	NA	NA	4049	NA	2457	LC	Medium	47	2 5	1	0	0	0	1	0	0	0	0	1	1	900 - 3780	0	0	0

Zoothera tanganjicae	NA	NA	NA	NA	NA	NA	NA	NA	LC	High	41	2	1	0	0	0	1	0	0	0	0	1	0	1310 - 3600	0	0	0
Zosterops senegalensis	NA	NA	2857	3157	2568	3399	3184	NA	LC	Low	4	2 5	1	0	0	1	1	0	0	0	1	1	0	0 - 1600	0	0	0

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