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The Global Macroecology of Penguin Distribution and Conservation

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Research

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“The greater danger for most of us
lies not in setting our aim
too high and falling short,
but in setting our aim too low and
achieving our mark.”

-Michelangelo

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Publications and Outputs

Scientific Papers

Hickcox R.P., Jara M., Deacon L.A.K., Harvey L.P., & Pincheira-Donoso D. (2015) The global macroecology of penguin distribution and conservation: it's not all happy feet. To be submitted.

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Pincheira-Donoso D., Jara M., Harvey L.P., **Hickcox R.P.**, Deacon L.A.K., Escobar L.E., & Qiao H. (2015) Rapid niche evolution in a globally expanding vertebrate species: large-scale adaptive radiation in the Anthropocene. To be submitted to *Nature Communications*.

Deacon L.A.K., Jara M., **Hickcox R.P.**, Harvey L.P., & Pincheira-Donoso D. (2015) The macroecology of geographic range size evolution from the perspective of a lizard adaptive radiation. To be submitted to *Global Ecology and Biogeography*.

Conference Presentations

Hickcox R.P. (2015) The global macroecology of penguin distribution and conservation: it's not all happy feet. EU Macro Conference Ignite Presentation, Copenhagen, Denmark.

Hickcox R.P. (2015) The global macroecology of penguin distribution and conservation: it's not all happy feet. University of Lincoln, UK.

Contributions

During my MRes I worked on four scientific papers, the first of which (Chapter 1, below) is the core research of my degree. I collaborated on three other papers (Appendices 1 to 3, below) which are currently submitted or ready to be submitted to major peer-reviewed journals. I describe my contribution (and my collaborators' contributions) to these papers below.

Chapter 1: The global macroecology of penguin distribution and conservation: it's not all happy feet

Design of study: **RPH**, DPD; data collection: **RPH**; data analysis and interpretation: **RPH**, MJ; wrote manuscript: **RPH**; project supervision: DPD; All authors (**RPH**, MJ, LAKD, LPH, DPD) discussed the results and implications and edited and commented on the manuscript at all stages.

Appendix 1: Evolutionary loss of precloacal signalling glands in a lizard radiation: do multivariate climatic factors hold the key?

Design of study: DPD, MJ; data collection: DPD; wrote manuscript: DPD. All authors (**RPH**, MJ, LAKD, LPH, DPD) performed data analysis and interpretation, discussed the results and implications, and edited and commented on the manuscript at all stages.

Appendix 2: Rapid niche evolution in a globally expanding vertebrate species: large-scale adaptive radiation in the Anthropocene.

Design of study: DPD, MJ; wrote manuscript: DPD; All authors (**RPH**, DPD, MJ, LPH, LAKD, LEE, QH) performed data analysis and interpretation, discussed the results and implications, and edited and commented on the manuscript at all stages.

Appendix 3: The macroecology of geographic range size evolution from the perspective of a lizard adaptive radiation.

Design of study: LAKD, DPD; data collection: DPD, LAKD; data analysis and interpretation: LAKD, MJ, DPD; wrote manuscript: LAKD; project supervision: DPD. All authors (**RPH**, LAKD, MJ, LPH, DPD) discussed the results and implications and edited and commented on the manuscript at all stages.

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Part 1: Primary Research

Part 1 comprises the primary research of this MRes thesis, focusing on the global distribution of all 18 penguin species to determine if current conservation methods effectively protect their species stability and biodiversity. **This is the core research conducted during my MRes.**

Chapter 1

The global macroecology of penguin distribution and conservation: it's not all happy feet

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Abstract

Current global biodiversity crises have reinforced the urgency to accurately quantify macroecological patterns of species distributions with the aim to develop efficient evidence-based protection strategies. The establishment of protected areas (PAs) is one of the major approaches to mitigate biodiversity declines during the Anthropocene. However, the distribution of biodiversity (e.g., hotspots, threatened species) is spatially asymmetric among regions and lineages, and the extent to which PAs offer an effective method for species and ecosystem protection remains uncertain. Penguins, broadly regarded as prime indicators of environmental health, are emerging as priority organisms for such quantitative assessments. The vast majority of all 18 penguin species are suffering population declines, and 11 of them are considered vulnerable/endangered given environmental and anthropogenic threats. However, how protected are penguins globally? Using spatial ecology approaches, we create novel distribution, hotspot, and endemism maps for all penguin species on Earth. We use these data to quantitatively assess the protection offered by PAs validated by the International Union for Conservation of Nature (IUCN) and other national/international organizations. We then create a universal target protection model which predicts the appropriate protection level required for each individual species based on population and range size (both predominant factors underlying population stability). For six species, less than 20% of their range is protected. PAs are only related to range size, whereas other parameters critically linked to population stability such as population size and IUCN conservation status are insignificant. Half of the nine global hotspots of penguin diversity are underprotected, and protection for 10 species is less than the calculated target protection. Consequently, global protection of penguins is not satisfactory. We suggest that more comprehensive ways to account for the multi-dimensional interactions between areas and organisms are needed to further the effectiveness of PA networks.

Introduction

As the impact of human-induced threats to global ecosystems escalate, the quantification of large-scale ecological patterns and drivers of biodiversity distribution has become a vital conservation priority with major scientific, social, political, and ethical implications (Boersma & Parrish 1999; Hannah & Lovejoy 2005). In recent decades, anthropogenic threats to terrestrial wildlife, mainly climate change, habitat destruction, and exploitation of natural resources, have become increasingly prevalent as drivers of rapid decline and extinction of biodiversity at both spatial and taxonomic scales (Dirzo *et al.* 2014; Trathan *et al.* 2014). These global crises linked with biodiversity loss have led to the establishment of protected areas (PAs) around the world. PAs are designated with the long-term aim to sustainably mitigate human impacts on ecosystems by restoring historical ecological processes and preventing future anthropogenic damage to biodiversity (Brooks *et al.* 2004; Moilanen *et al.* 2009; Bertzky *et al.* 2012). However, a major characteristic of biodiversity is its spatial and phylogenetic asymmetry (Reid 1998; Myers *et al.* 2000; Orme *et al.* 2005; Gaston *et al.* 2008). One of the central challenges faced by the PA approach is the identification of vulnerable or irreplaceable geographic regions that take into account the features of resident biodiversity (e.g., endemism, species richness, taxonomic uniqueness).

Over the last six decades, PAs have generally been considered as an effective conservation approach, because they encompass areas and organisms which have been prioritized for conservation actions based on ecological indicators (Reid 1998; Boersma & Parrish 1999; Pichegru *et al.* 2010; Bertzky *et al.* 2012; Dirzo *et al.* 2014; Trathan *et al.* 2014). For instance, many PAs have resulted from prioritizing the protection of biodiversity hotspots, including areas with high species richness or endemism (Myers *et al.* 2000; Thiollay 2002; Brooks *et al.* 2006; Trathan *et al.* 2014). In addition, conservation prioritization must account for interactions between species-level parameters such as range size and population size, both fundamental to species stability. For example, species with larger geographic ranges are more likely to be exposed to multiple, local-scale ecological pressures (i.e., heterogeneous natural selection across their range) and thus experience local adaptations to some extent (Gaston 2003). As a result, these species may be able to maintain genetic diversity and spatial persistence if part of their ranges are altered, which may ultimately minimize their requirement for conservation initiatives (Frankham 1996; Gaston 2003; Höglund 2009; Charlesworth & Charlesworth 2010). Therefore, the effects of range and population size can highlight lineages that require more urgent protection.

As a compliment or subsequent action to prioritization, PAs are categorized by various international and national schemes in order to create a cohesive PA network.

The International Union for Conservation of Nature (IUCN), the leading global environmental organisation, created a PA category system based on management objectives and legal status (IUCN 2001; Dudley 2008). The purpose of this category system is to provide stakeholders with a framework for managing, reporting, and monitoring PAs. PAs are nationally or locally designated and categorized using this IUCN system. Thus, the role of IUCN is essentially as a consultant, not an enforcer, of the PA category system. Alternatively, some PAs such as World Heritage sites are managed by international stakeholders. The differentiation between types of PAs is an important indicator of PA management and the overall effectiveness of PAs at preserving biodiversity. When assessing the irreplaceability of a species and its vulnerability to biodiversity loss, it is now imperative to consider how PA classification affects the overall effectiveness of the PA (Pressey *et al.* 1994; Pressey & Taffs 2001; Dudley 2008). Different categorization systems may cause a difference in the levels of protection, and these strategies must be continuously adapted in order to remain effective against enduring threats and perpetual environmental change. Overall, PAs have become the most widely implemented conservation strategy (Gillingham *et al.* 2015), and as of 2014, 15.4% of global terrestrial areas and 3.4% of ocean areas (of which 0.94% are no-take reserves) were protected (Juffe-Bignoli *et al.* 2014; Marine Conservation Institute 2015).

A prime example of taxonomically unique organisms encompassing critical ecological features considered in conservation decisions are penguins. Penguins, broadly regarded as wildlife and cultural icons, are represented in the public climate change and conservation movements as focal targets for protection. These distinctive birds, comprising of 18 species globally, are primarily restricted to the southern hemisphere (the only exception being *Spheniscus mendiculus* from the Galápagos Archipelago). Approximately two-thirds of penguin species are experiencing major population declines (Borboroglu & Boersma 2013; Boersma & Rebstock 2014; Trathan *et al.* 2014). The conservation status of 11 out of 18 species is Vulnerable or Endangered, as defined by the IUCN Red List of Threatened Species (i.e., Least Concern, Near Threatened, Vulnerable, or Endangered) (Ellis 1999; Boersma 2008; IUCN 2014). Penguins are dependent on and constrained to limited areas of the ocean for foraging and land for breeding. Typically, foraging ranges are influenced by prey availability, and colonial breeding occurs annually at the same location (Boersma 2008), which results in temporal and spatial variability of threats. Anthropogenic drivers of population declines include habitat loss, commercial fishing, oil spills, guano harvesting, pollution, and tourism, whereas environmental threats include climate change, invasive species competition, El Niño events, and predation (Borboroglu *et al.*

2008; Gandini *et al.* 2010; Pichegru *et al.* 2010; Borboroglu & Boersma 2013; Trathan *et al.* 2014). While the most severe threats may be marine (i.e., overfishing and bycatch), terrestrial threats have direct negative effects on the reproduction and survival of penguins, such as tourism and habitat modification (Trathan *et al.* 2014), making terrestrial conservation efforts vital for penguin survival.

Penguin populations respond rapidly to various environmental and anthropogenic pressures, reflecting local terrestrial and marine environment variability, quality, and stability (Boersma 2008; Borboroglu *et al.* 2008; Trathan *et al.* 2014). While some species have widespread distributions and high population densities, others have highly restricted ranges (Fig. 1), which likely increases their vulnerability to environmental change. For example, species experiencing the highest population declines, such as *Spheniscus demersus*, are those with restricted distributions and high exposure to human-induced environmental alterations. In contrast, species with the largest population and range sizes breed in Antarctica and are relatively undisturbed by humans (Borboroglu & Boersma 2013). To evaluate the current effectiveness of penguin conservation strategies and guarantee their future success, we must begin by analysing the ecological components used to prioritize and categorize sites and species across different PAs systems.

In this paper, we investigate for the first time the extent to which multiple aspects of global penguin ecology overlap with conservation strategies. We aim to address whether (i) the terrestrial geographic distribution of global penguin species is sufficiently protected by existing PAs, (ii) species with higher levels of protection are categorized as more threatened or are biologically more likely to experience population declines (e.g., smaller ranges or population sizes), and (iii) hotspots of penguin biodiversity (species richness and endemism) fall within existing PAs. Additionally, we develop a target model to estimate the ideal PA coverage for each species based on their range and population size. PAs are effective for conservation and provide a foundation upon which they can be expanded and consolidated. However, a more decisive, universal measure is needed for determining how much protection is required to recover a threatened population or prevent a population from becoming threatened.

Methods

Species data

Penguin colonies tend to be temporally and spatially consistent in location and population, while foraging distribution changes rapidly due to external factors such as

prey availability and weather patterns. Also, little is known about the foraging behaviour of penguins, so we focused on terrestrial PAs and colony distribution instead of marine PAs and distribution. We compiled a global scale dataset of the terrestrial geographic distribution of all 18 known penguin species based on GPS coordinates from two databases. Ocean Biogeographic Information System (OBIS 2014) provided 233,627 data points for Spheniscidae, and Global Biodiversity Information Facility (GBIF 2013) provided 121,279 data points for Sphenisciformes. Additionally, we included 412 data points from Borboroglu and Boersma (2013), the most recent published compilation of colony coordinates. We then removed duplicate records between databases, spatial records of individuals free-ranging in the ocean, and fossil/dead specimen records, resulting in a final dataset of 19,690 individual records encompassing the whole diversity of known extant penguins. Data on population size and conservation status were obtained from Borboroglu and Boersma (2013) and are a compilation of published and unpublished data from many sources. As expected, population size is naturally variable, and although there is no universal technique to count individuals in a penguin colony these population estimates are the most complete and accurate to date based on satellite imaging and long-term data collection.

Protected Areas data

We employed GIS shapefiles provided by the World Database on Protected Areas (WDPA), which is managed by IUCN and the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) (IUCN & UNEP 2014). We first analysed IUCN PAs, classified as I-VI by the IUCN Protected Areas Categories System, the world's most inclusive and globally accepted prioritization scheme for nationally managed PAs (Table 1, see Dudley (2008) for further descriptions). As defined by IUCN, PAs are terrestrial or freshwater environments grouped according to their natural, ecological, and/or cultural attributes (Bertzky *et al.* 2012; UNEP-WCMC 2012).

In addition to IUCN PAs, we investigated areas that are nationally protected but not categorized ("Not Reported", NR) and international PAs ("Not Applicable", NA) (UNEP-WCMC 2012). We also considered all land south of 60 degrees latitude to be a single Antarctica PA. According to the Antarctic Treaty (AT) System, the whole of Antarctica is a large natural reserve, similar to IUCN PAs in category Ia or II (Protocol on Environmental Protection to the Antarctic Treaty 1991). The single Antarctica PA, NR, and NA PAs were grouped as "Not Categorized" (NC) in our analyses.

PA coverage was calculated using the 2014 WDPA shapefiles and corresponding attribute tables. Due to the ambiguity of particular records, all point

records, those with null latitude and longitude, those listed as “marine”, polygon records with no area information, and those north of the Equator were excluded from these analyses. Some areas are classified using both IUCN and other category systems simultaneously, so overlap between different designation types was removed when determining the total protection for each species. In total we considered 24,080 PA records.

Species distribution analyses

We mapped the global terrestrial distributions of penguin colonies for all species against the spatial distribution of PAs. Colonies vary temporally and spatially in population and range size. Although they have high nest site and colony fidelity, penguins adapt to environmental change and anthropogenic pressures by abandoning or forming new colonies (Ainley *et al.* 1995). Therefore, we accounted for this spatial fluidity and calculated each species' range size, rather than the more unstable measure of colonies at a given point in time, based on the extent of occurrence (outermost limits of an area over which a species actually occurs; EOO) using a modified Minimal Polygon Convex method (IUCN 2001; Gaston 2003; Gaston & Fuller 2009). We then created terrestrial distribution polygons by using the coastline as one boundary and 10 km inland as the other boundary. The 10 km boundary, the average distance travelled from breeding colony to the ocean by all penguin species, was adjusted to the distribution points to eliminate unoccupied areas. For Antarctica, we used a boundary of 100 km because the five species of Antarctic penguins (*Aptenodytes forsteri*, *Eudyptes chrysolophus*, *Pygoscelis adeliae*, *Pygoscelis antarctica*, *Pygoscelis papua*) travel an average of 100 km from breeding colony to the ocean (Borboroglu and Boersma 2013). Although the polygons may include areas not currently occupied by breeding penguins (e.g., area between colonies, geographic features), this method best represents unrecorded colonies, potential future colonies, and areas used by penguins for non-breeding purposes. We estimated IUCN, NC, and total protection coverage by masking and clipping all PAs, including Antarctica, using each species' EOO. We then quantified the overlap of each PA (in km²) within all species ranges. We performed all analyses using the Analysis and Spatial Statistics tools of ArcGIS 10.2.2 (ESRI 2014).

Species richness and endemism analyses

After creating a GIS grid shapefile of global penguin distribution with the southern hemisphere as a mask and a cell size of 1 degree (~111.12 km at the Equator), we

constructed the distribution of species richness of penguins (i.e., number of species contained per single grid cell) using Spatial Analysis in Macroecology (SAM) software, available at <http://www.ecoevol.ufg.br/sam> (Rangel *et al.* 2010). We considered as hotspots those grid cells in which four or five breeding species have been recorded, which represents the richest 2.5% cells (Orme *et al.* 2005). We then determined the overlap between worldwide biodiversity hotspots, as established by Myers *et al.* (2000), and penguin ranges to quantify the extent to which a species range within a biodiversity hotspot is protected.

Additionally, we investigated whether hotspots of endemism are associated with PAs. According to Crisp *et al.* (2001), a species is endemic if it occurs only in a defined area (i.e., continent, region, or ecoregion). An area has high endemism if it contains many range-restricted species. We first determined which penguin species are endemic to global terrestrial ecoregions, representative of distinct biotas and likely reflecting species distribution (Olson *et al.* 2001). By overlaying ecoregion polygons (an ArcGIS layer package) with penguin ranges, we identified all ecoregions within which a species is located. We considered a species endemic to an ecoregion if that species is found only in that ecoregion. To determine global endemism, we first calculated the Corrected Weighted Endemism (CWE) for each grid cell, in order to reduce the strong effect of species richness and emphasize areas that have a high proportion of species with restricted ranges. CWE represents the weighted endemism (for each grid cell, the sum of the reciprocal of the total number of grid cells that each species occurs in) divided by the total number of species in that cell (Crisp *et al.* 2001). This index ranges from 0.0 to 1.0, corresponding to 0-100% of the species occurring within that cell are range-restricted to that cell (Laffan & Crisp 2003). We performed all analyses using the Analysis and Spatial Statistics tools and SDMTtoolbox (CWE) of ArcGIS 10.2.2 (Brown 2014; ESRI 2014).

Protected area targets

Previous methodologies have solely used species range size to calculate target levels of PA coverage to determine whether a species is sufficiently protected (Rodrigues *et al.* 2004a; Thuiller *et al.* 2015). However, this method ignores population size, a major factor underlying vulnerability to extinction (Ferrière *et al.* 2004; Höglund 2009). For penguins, population size is positively correlated with range size (Spearman's Rank Correlation, $r_s = 0.51$, $P = 0.04$). To control for this confounding variable, we created a new model to predict the ideal amount of a species range that should be covered by a PA to be considered effectively protected (hereafter referred to as "protection target"). Expanding from the previously developed model by Rodrigues *et al.* (2004a), we first

calculated the residuals of a linear regression of the independent variable range size and the dependent variable population size. Using residuals allows for the quantification of the relationship between population and range size. We then set the maximum target of 100% coverage for those species with residual values within the 10% quantile (i.e., species with the smallest range/population residuals; low population density). A minimum target of 17% coverage was used for those species with residual values within the 90% quantile (i.e., species with the largest range/population residuals; high population density). This minimum target was based on the Aichi Biodiversity Targets, part of the Strategic Plan for Biodiversity 2011-2020, which declares that at least 17% of terrestrial and 10% of coastal and marine areas should be protected by 2020 (Brooks *et al.* 2004; Convention on Biological Diversity 2010; Bertzky *et al.* 2012; Venter *et al.* 2014). Although aimed at the protection of terrestrial regions, we are supplementing Target 11 as the universal target for species protection due to the lack of protection targets for individual species. To determine targets for species with intermediate residuals, the target maximum and minimum (100% and 17% respectively) were regressed with the upper and lower limit residuals (90% and 10% quantile values respectively). Thus, the amount of protection required for each species can be estimated using the linear model equation $y = -0.00002x + 65.058$ (Rodrigues *et al.* 2004a; Thuiller *et al.* 2015).

Quantitative analyses

To address whether existing PAs are related to several biodiversity factors, we first employed linear and quadratic regression analyses, respectively, to quantify the relationship between population and range size between different types of PAs. Population and range size data was log transformed ($\ln+1$), although transformation did not change non-normal distribution. A Kruskal-Wallis one-way ANOVA was performed to determine whether protection levels differed among IUCN conservation statuses (i.e., Least Concern, Near Threatened, Vulnerable, and Endangered). We then evaluated whether there is an association between range size and conservation status by using ANCOVA and controlling for the effects of the covariate population size. Finally, we used a combination of regression analyses and Wilcoxon Rank Sum tests to determine target protection based upon the residual model. All statistics were implemented in R version 3.1.2 (R Development Core Team 2014) and SPSS version 21.0 (IBM Corporation 2012).

Results

Global species distributions

Penguin species are widely distributed across four continents and occupy a global area of 57,326,119 km² (Fig. 1). Geographic range sizes vary dramatically across species (Table 2, Fig. S1 in Supporting Information). There is a significantly skewed tendency for range sizes to be small (Shapiro-Wilk, $P = 0.003$), with the smallest range being only 7.64 km² (*Eudyptes robustus*) and the largest being 2,336,709.09 km² (*A. forsteri*). Individual species ranges can span a large portion of the Antarctic coast (*P. adeliae*) while others are restricted to a small island (*E. robustus*).

Protected area coverage

All penguin species are protected to some degree (see Fig. S2 for PA map) by at least one PA (Table S1), and that protection differs significantly between IUCN and NC (Wilcoxon Rank Sum, $W = 57$, $n = 18$, $P = 0.009$). Total protection varies from 6.48% (*Spheniscus humboldti*) to 100% of a species range. For six species, total protection is greater than 50%, and an additional six species are fully protected by IUCN and NC PAs (disregarding Antarctica, only *E. robustus*, *Eudyptes schlegeli*, and *Eudyptes sclateri* are fully protected; Table 2). More specifically, IUCN protection ranges from 0% to 100%, and six out of 18 species are protected by more than our 17% target by IUCN. NC PAs cover 13 species by more than 24%, while the remaining species are protected less than 13% (Fig. 2). Additionally, some areas are protected simultaneously by IUCN and NC (Table S2). For example, *S. mendiculus* is 96.32% and 96.40% protected by IUCN and NC, respectively. However, the total combined protection is 97.33%, indicating an overlap of 95.40% (Fig. 2).

A regression analysis revealed that there is a significant relationship between NC and total PA coverage and range size (Table 3, Fig. 3). Species with small or large ranges are more protected by NC PAs than those species intermediate ranges. Conversely, species with intermediate ranges are more protected by IUCN PAs, although this relationship is non-significant. Population size and conservation status have non-significant relationships with PA coverage (Table 3). Additionally, conservation status is significantly influenced by range size but not population (Fig. S3). Endangered and Vulnerable penguins are more protected and have significantly smaller ranges sizes and non-significantly smaller population sizes (Fig. 2, Fig. S3). IUCN protection focuses on Vulnerable and Endangered species, while NC protection remains similar between status levels. When accounting for population as a covariate,

there is no significant difference in range size and conservation status (ANCOVA, $F_{3,10} = 3.11$, $P = 0.06$).

Hotspots of species richness and endemism

Our analyses identify nine global hotspots of penguin biodiversity concentrated in the South Pacific, southern tip of South America, and Antarctic Peninsula (Fig. 4a, Table S3). Of these hotspots, three are fully protected by the AT, three are fully protected by IUCN and NC PAs, and the South Georgia/South Shetland Islands are fully protected by both IUCN and the AT. Furthermore, penguin hotspots do not significantly overlap with biodiversity hotspots (Fig. 4a). Approximately 1.49% of total penguin range is within a biodiversity hotspot, and 30.48% of that area is protected. Out of the 12 species whose ranges are within a biodiversity hotspot, nine overlap with a hotspot by more than 60%. The remaining six species are entirely excluded from a biodiversity hotspot. Additionally, range size and population size are significantly related with biodiversity hotspot overlap and protection (Table 2). Species with smaller range and population sizes not only overlap biodiversity hotspots significantly more than those species with larger ranges and population sizes but are also more protected within the biodiversity hotspot (Fig. 3).

Globally, CWE ranges from 0.0 to 0.6. Species found in New Zealand, Australia, and on several Southern Atlantic islands and the Galápagos tend to be highly endemic (Fig. 4b). Out of a total of 867 ecoregions, penguin species are found in only 12 (Olson *et al.* 2001) and 5 species are endemic to a single ecoregion (Table 2).

Protected Area targets

The protection target model (Fig. 5) calculated that seven species should be fully protected and nine should be protected by more than 37% (Table 2, Fig. 2). The difference between the target levels and the actual total protection levels are significantly different (Wilcoxon Rank Sum, $W = 324$, $P < 0.001$). On average, an additional 1,105,008.27 km² of total penguin range should be protected in order to reach the target protection level of 75.18% for all penguins (Fig. 6, Table S4).

Discussion

Our study provides the first quantitative analyses investigating the relationships between global macroecological patterns of penguin distributions and existing PAs. This approach stresses the increasingly vital role of macroecological perspectives to

identify general patterns underlying the interactions between species distributions and their population dynamics. In a rapidly changing world, the identification of such patterns will allow evidence-based predictions about the magnitude and impact of anthropogenic threats on species, ideally influencing the decisions about environmental management. Therefore, our study fills an integral gap in the knowledge of these global interactions experienced by penguins, one of the most iconic groups of vertebrates on Earth.

The main purpose of PAs is to isolate representative elements of biodiversity from threatening processes and promote their persistence. Although 61% of the total global penguin range is protected by IUCN and NC combined, statistically speaking PA coverage is extremely variable and unpredictable among species, with no standardisation based on conservation status or population size. In addition, the small number of hotspots and the tendency for penguins to be highly endemic to a small number of ecoregions is likely to increase species risk of decline under environmental or population changes. Previous analyses of the irreplaceability and vulnerability of penguins (Borboroglu & Boersma 2013; IUCN 2014) combined with our findings, highlight our concerns about the generality and inadequate coverage of global PAs and support our advocacy for improved prioritization of sites and species.

Protection efficiency: PAs, hotspots, and 'coldspots'

PAs ensure the persistence of nature by primarily limiting the effects of humans on species and habitats. However, simultaneous management by more than one organization or the categorization as different types of PAs highlights the overall mismanagement and non-collaborative designation processes. For example, the Galápagos Islands are classified as a World Heritage site, a UNESCO-MAB Biosphere Reserve, a Ramsar site, and an IUCN national park (Table S2). Although the Ecuador government manages the islands, each type of PA has its own prioritization strategy, goals, and management objectives, resulting in conflicting category rankings and overall protection of the PA. This also highlights the implications of classification by different bodies in general. Every category has its own conservation priorities, and every organization and stakeholder has different motivations and strategies. The disparity between being classified as a PA and the actual conservation of that area can be evident when assessing PA effectiveness. Moreover, what happens after a PA is designated an IUCN category? Once a PA is classified, the designating body (usually local or governmental stakeholders) is responsible for reporting all available data to IUCN, ensuring legal legitimacy, and monitoring ecological and environmental change over time. In essence, there is no guaranteed way to ensure all PAs are indeed

protected. Because of IUCN's noninterfering approach, there is currently no enforcement of the PA guidelines and no institution to hold stakeholders accountable. While there have been great advancements toward the creation of a unified classification scheme, there is still a considerable incongruence between classification and management.

In this analysis, we included Antarctica (areas protected by the AT) because of its similarity to other PAs defined by IUCN categories. Indisputably, the AT does not protect penguin foraging areas or prey populations. However, its terrestrial effectiveness as a politically neutral scientific preserve protecting penguin breeding areas to some extent justifies it as a PA (Protocol on Environmental Protection to the Antarctic Treaty 1991). Similar to the inclusion of Antarctica, our ranges include areas that are not currently occupied by penguin colonies. Although these methods may overestimate protection, it systematically considers the spatial variability of penguin colonies and includes areas that may be colonized as a result of environmental adaptation, an unequivocally important component of PA design.

If we consider the primary conservation goal to be preserving biodiversity in all forms, preventing extinctions (the greatest process affecting global biodiversity) is the most critical action (Eken *et al.* 2004; Brooks *et al.* 2006; Akçakaya *et al.* 2007; Dirzo *et al.* 2014). For this reason, conservation focuses on protecting areas that support the largest number of species having the smallest, most threatened populations. This is especially true for penguins. Populations are generally small with relatively small breeding areas confined to coastal zones. More specifically, because only 18 penguin species exist, the loss of even a few populations could potentially be detrimental to the entire family. Alternatively, the protection of biodiversity 'coldspots' containing only one species may be preferable if that species is endemic (Orme *et al.* 2005). For example, *S. mendiculus* live only on the Galápagos Islands and are, debatably, distinct from other penguin species due to rarity and ecological adaptations such as heat tolerance. Being the only tropical species of penguins and the only species to live on the Equator, *S. mendiculus* is a recent divergence of the whole lineage aided by the cool Humboldt Current (Baker *et al.* 2006). They provide valuable information about diversification and adaptation of heat tolerance, a key concern with current rates of global warming and an exclusive evolutionary event within the entire family. They also have a naturally small population size and range size. Any significant population loss could result in the eventual extinction of the whole species. Species convergence within an area and the interaction between species richness and endemism make it difficult to determine which penguin species to protect in order to simultaneously maintain genetic, species,

and ecosystem diversity. Therefore, protection should consider both environmental conditions and behavioural ecology in order to be inclusive of a species biodiversity.

PA target model

The current global target for terrestrial PA coverage, as identified by the Aichi Target 11, is 17% (Brooks *et al.* 2004; Bertzky *et al.* 2012; Venter *et al.* 2014). This is a static target unified across all areas and cannot be accurately applied to individual species because it does not consider variation in biodiversity factors. Therefore, we have established a framework to determine the ideal PA coverage for each species.

Based on our model, actual protection for Endangered and Vulnerable species is less than the calculated PA targets, while the inverse is true for Least Concern and Near Threatened species. The magnitude of difference between total and target protection is also greatest for Endangered and Vulnerable penguin species (Fig. 6), showing a need for greater protection of those more threatened species. Interestingly, this difference can also be interpreted as a result of prior protection. It is possible that species may be considered less threatened because they are more protected. Therefore, it is justified to assume that conservation status may change for these species if protection decreases.

Our target model is an effective tool for spatial prioritization, because it incorporates the ecology of the target organisms. Such a model depends on quantitative information about an organism, such as range and population size. However, variability in population size creates uncertainty in the model, but can be accounted for by frequent re-analysis using current population sizes or by creating target ranges (e.g., 60-65% protection) using the largest and smallest estimated population sizes. For a more robust model, inclusion of qualitative and interpretive measures of ecology such as threat level, conservation status, and vulnerability should be included, but this requires a more standardized, measurable evaluation method to make it consistent across all species (Moilanen *et al.* 2009). This target model could also be adapted to any taxa and used to implement more refined and representative PAs.

Future protection of penguins

PA categorization influences conservation actions and results. Here we examine how the difference in the terrestrial protection of penguins is affected by PA categories. However, due to the inconsistent nature of PAs (i.e., unequal reporting and monitoring), we were unable to evaluate the effectiveness of PAs in maintaining stable

populations of organisms. Our findings are thus restricted to summarizing which types of PAs protect penguins but not how well they protect them. Macroecological studies are therefore most useful for examining the PA system as a whole and on larger scales; future, more microecological studies would be more appropriate to assess the ground-level outcomes from PAs.

In theory, sites for conservation should be prioritized following the identification of vulnerable and irreplaceable ecosystems and species. However, in practice, prioritization tends to be (primarily) geographically or taxonomically designated, with no clear systematic connection (Bertzky *et al.* 2012). This is the case for penguins. Existing PAs often do not include species for which conservation is needed the most (Eken *et al.* 2004). Furthermore, protection can be focused proactively or reactively, depending on management objectives. An area can be prioritized in order to prevent future biodiversity loss or repair loss that has already occurred. Because the majority of penguin species are highly threatened, have small ranges and population sizes, or are endemic to small regions, we propose a combination of both proactive and reactive conservation strategies. Species experiencing threats or large population declines, in addition to biodiversity hotspots (specifically the Falkland Islands, Tierra del Fuego, and Southern New Zealand), should be considered for increased protection and future PA implementation. Furthermore, additional assessments of the effectiveness of the AT and marine PAs at protecting penguin marine foraging areas and prey are required for the global conservation of all areas vital to penguin survival.

Conclusion

Over the past three decades, the increasing global biodiversity crises arising as a result of human activities have promoted exponential growth in the development of ecologically- and evolutionary-based conservation approaches (Ferrière *et al.* 2004; Höglund 2009). These methods rely primarily on PAs aimed to mitigate the impact of rapid alterations to ecological interactions of species with their ecosystems (Gaston *et al.* 2008). Although some PAs maintain and increase biodiversity by promoting processes such as migration and proliferation (e.g., improving habitat connectivity, reducing fragmentation, limiting poaching) (Thomas & Gillingham 2015), they are generally failing to protect key species (Gaston *et al.* 2008). There is high variability in the ecological performance of PAs and the disparity between populations within and outside of those areas (Boersma & Parrish 1999; Rodrigues *et al.* 2004b; Hoekstra *et al.* 2005).

From our findings, we suggest future research should focus on the quantification of colony-level processes to generate a “micro-macroecological”

understanding of how intraspecific processes of colony dynamisms shape the nature of species as a whole. An integrative approach which distinguishes species-level patterns based on colony-level dynamics can identify the specific conservation requirements of a species and the need for modifiable conservation strategies. In particular, PAs should be assessed based on population size to account for the variability between colonies. Protection requirements and conservation needs for species and population sustainability within each PA should also be determined. Management and policy should be assessed to distinguish between effective and non-effective PAs, so that future evidence-based policy, including global promotion of IUCN category system can then be implemented. A precedent is required for managing PAs, and a universally robust framework must be developed to clearly identify which species and areas need to be conserved.

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Table 1: IUCN PA category names and definitions

<p>Category Ia: <u>Strict nature reserve</u> Strictly protected for biodiversity and also possibly geological/ geomorphological features, where human visitation, use and impacts are controlled and limited to ensure protection of the conservation values</p>
<p>Category Ib: <u>Wilderness area</u> Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, protected and managed to preserve their natural condition</p>
<p>Category II: <u>National park</u> Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities</p>
<p>Category III: <u>Natural monument or feature</u> Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove</p>
<p>Category IV: <u>Habitat/species management area</u> Areas to protect particular species or habitats, where management reflects this priority. Many will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category</p>
<p>Category V: <u>Protected landscape/seascape</u> Where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values</p>
<p>Category VI: <u>Managed resource</u> Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management and where low-level non-industrial natural resource use compatible with nature conservation is seen as one of the main aims</p>

Table 2: PA and biodiversity hotspot coverage for each species classified by protection type, conservation status, population size, and range size. Calculated population/range size regression residuals and the target protection for each species based upon this residual model are included. Refer to Table S1 for complete PA coverage data.

Species	Ecoregion†	Status*	Population size	Range size (1,000 km ²)	Protection Level (%)				Biodiversity Hotspots (%)		
					IUCN	NC ‡	Total	Coverage	Protection	Residuals	Target Protection (%)
<i>Aptenodytes forsteri</i>	6,9	2	476,000	23336.71	0.03	100.00	100.00	0.00	0.00	-3447349.20	100.00
<i>Aptenodytes patagonicus</i>	2,4,6,9	1	3,200,000	94.77	20.04	24.55	41.56	5.66	5.25	1367193.10	37.71
<i>Eudyptes chrysocome</i>	2,4,6,7,9	3	2,460,000	220.14	5.82	13.72	17.95	0.97	0.97	615916.20	52.74
<i>Eudyptes chrysolophus</i>	2,4,6,9	3	12,600,000	240.74	8.48	34.17	41.11	0.00	0.00	10754063.60	17.00
<i>Eudyptes moseleyi</i>	4	4	530,000	0.40	2.08	61.73	61.73	0.00	0.00	-1294319.10	90.94
<i>Eudyptes pachyrhynchus</i>	2,4,5,7	3	6,000	110.27	29.00	42.49	45.65	65.40	35.07	-1828201.30	100.00
<i>Eudyptes robustus</i>	2	3	62,000	0.008	0.00	100.00	100.00	100.00	100.00	-1762283.40	100.00
<i>Eudyptes schlegeli</i>	6	3	1,700,000	0.38	100.00	100.00	100.00	100.00	100.00	-124317.00	67.54
<i>Eudyptes sclateri</i>	6	4	140,000	1.70	19.72	100.00	100.00	100.00	100.00	-1684435.30	98.75
<i>Eudyptula minor</i>	1,2,4,5,6,7,8	1	600,000	666.76	10.13	26.87	28.78	78.74	22.76	-1284256.10	90.74
<i>Megadyptes antipodes</i>	2,4,6	4	4,200	20.65	20.49	8.32	27.35	100.00	27.35	-1821940.10	100.00
<i>Pygoscelis adeliae</i>	6,9	2	4,740,000	19934.96	0.06	99.98	100.00	0.00	0.00	1122627.60	42.61
<i>Pygoscelis antarcticus</i>	6,9	1	8,000,000	11099.98	0.10	99.91	100.00	0.00	0.00	5177308.00	17.00
<i>Pygoscelis papua</i>	2,4,6,9	2	774,000	1032.39	1.57	85.07	86.30	0.00	0.00	-1143143.00	87.92
<i>Spheniscus demersus</i>	1,5,6,7,8	4	52,000	94.11	11.16	25.66	29.59	91.61	23.12	-1780747.40	100.00
<i>Spheniscus humboldti</i>	2,4,7	3	48,000	53.03	5.21	3.35	6.48	64.38	3.27	-1781052.80	100.00
<i>Spheniscus magellanicus</i>	1,2,3,4,7,9	2	2,600,000	411.21	12.17	11.53	18.99	25.11	6.15	738730.50	50.28
<i>Spheniscus mendiculus</i>	8	4	1,200	7.91	96.32	96.40	97.33	100.00	97.33	-1823794.40	100.00

* 1 Least Concern, 2 Near Threatened, 3 Vulnerable, 4 Endangered

† 1 Tropical and Subtropical Moist Broadleaf Forests; 2 Temperate Broadleaf and Mixed Forests; 3 Tropical and Subtropical Grasslands, Savannas and Shrublands; 4 Temperate Grasslands, Savannas and Shrublands; 5 Montane Grasslands and Shrublands; 6 Tundra; 7 Mediterranean Forests, Woodlands and Scrub; 8 Deserts and Xeric Shrublands; 9 Rock and Ice

‡ Not categorized

Table 3: Summary of population (linear, df = 1, 16) and range size (quadratic, df = 2, 15, denoted with †) regression and conservation status Kruskal-Wallis test (df = 3, denoted with ‡) for PA coverage and biodiversity hotspots. Coverage represents the percent of penguin ranges covered by a biodiversity hotspot, and Protection represents the total percent protection of these hotspots. Range size and population size data are transformed (ln+1).

	Predictor	Response	R^2	F	P
PA Coverage	Range size†	IUCN	0.22	2.17	0.15
		Not categorized	0.46	6.39	0.01*
		Total	0.45	6.046	0.01*
	Population	IUCN	0.12	2.37	0.14
		Not categorized	0.004	0.06	0.81
		Total	0.003	0.05	0.84
	Conservation Status‡	IUCN		$\chi^2 = 3.75$	0.29
		Not categorized		$\chi^2 = 0.55$	0.91
		Total		$\chi^2 = 0.74$	0.86
Biodiversity Hotspots	Range size†	Coverage	0.40	5.079	0.02*
		Protection	0.53	8.54	0.003*
	Population	Coverage	0.51	16.81	0.001*
		Protection	0.23	4.76	0.04*
	Conservation Status‡	Coverage		$\chi^2 = 5.91$	0.12
		Protection		$\chi^2 = 4.89$	0.18

*significant p-values

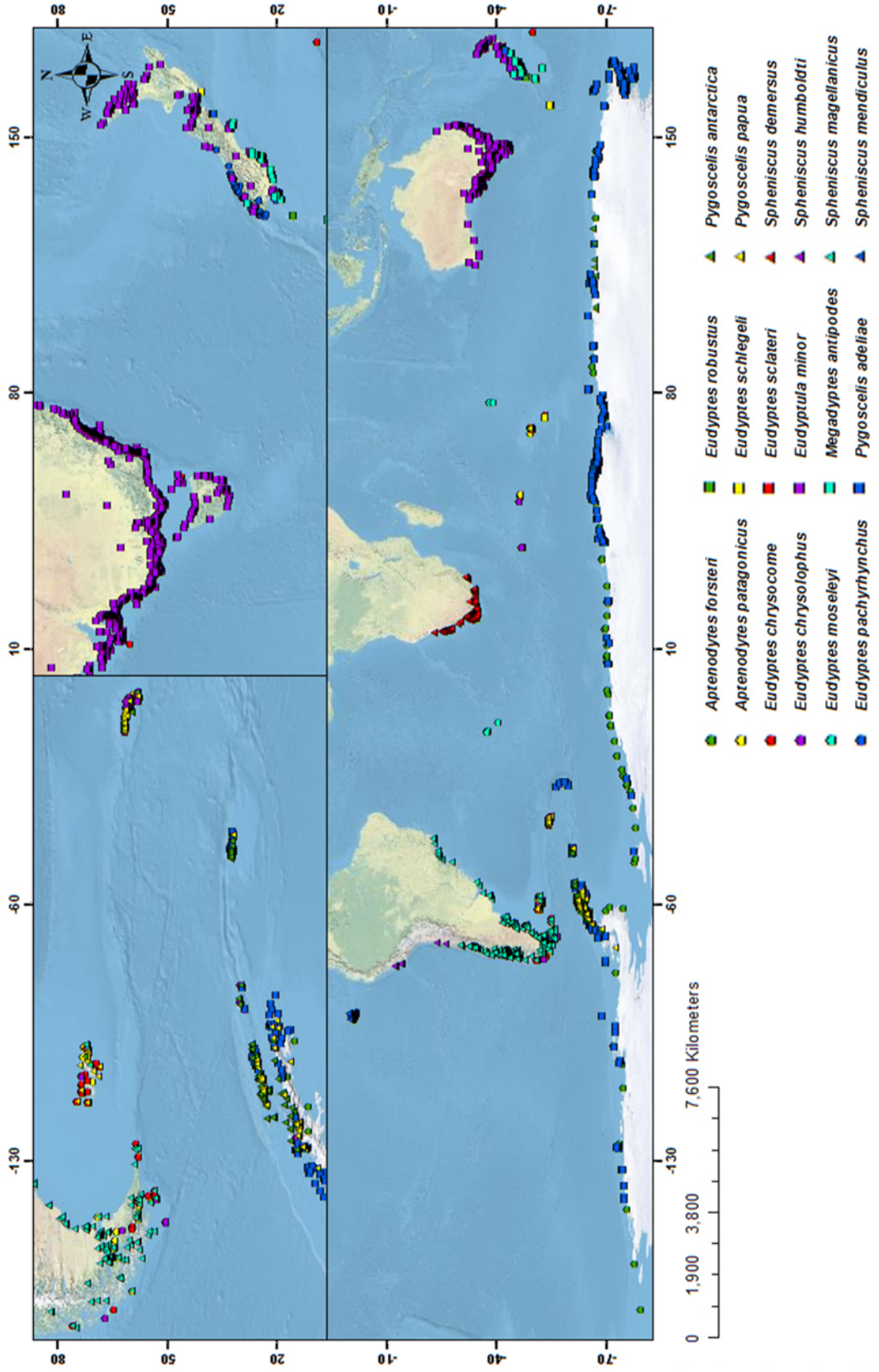


Figure 1: Global penguin and PA distribution map, projected using the World Geodetic System 1984.

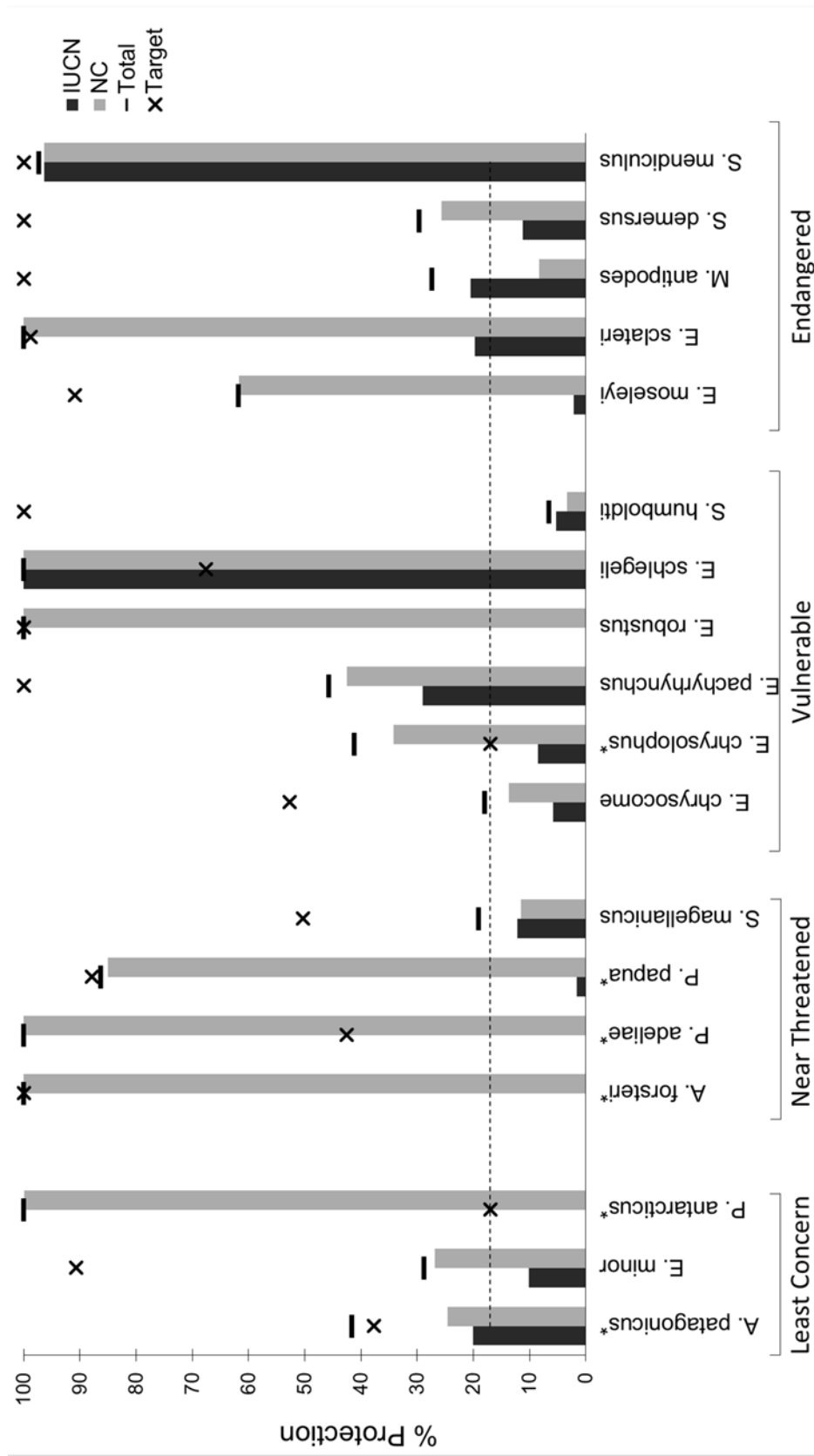


Figure 2: Percent IUCN (black bar), NC (grey bar), and Total (black horizontal line) protection for all species (Antarctic and sub-Antarctic species indicated by *), categorized by conservation status. The 17% global protection target (dashed line) and the calculated penguin protection targets (black x) are also shown.

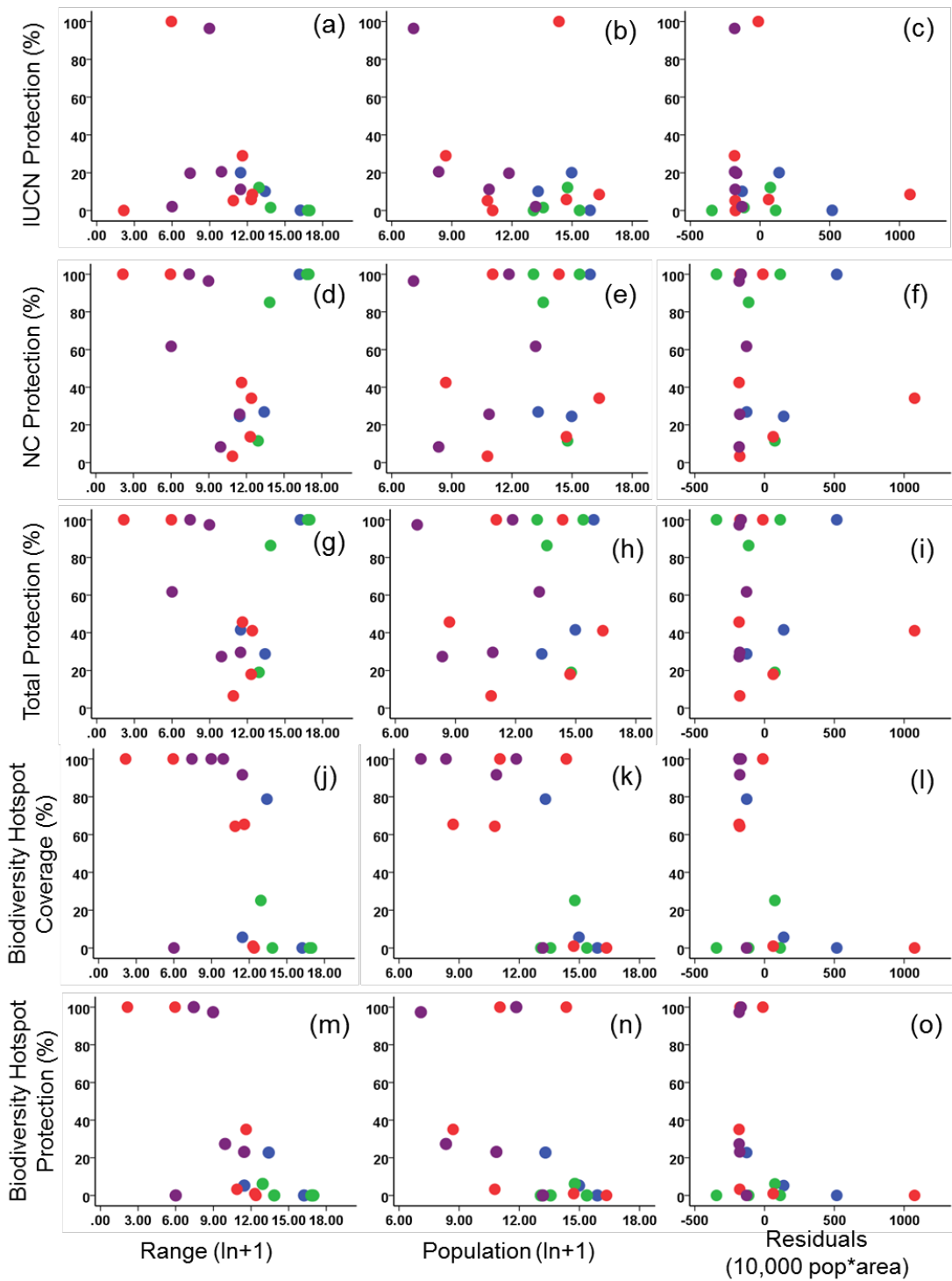


Figure 3: Pattern of protection based on range size (transformed), population size (transformed), and regression residuals. Blue = Least Concern, green = Near Threatened, red = Vulnerable, purple = Endangered. Included are graphs for (j-l) biodiversity hotspot coverage (percent that the biodiversity hotspot covers penguin ranges) and (m-o) biodiversity hotspot protection (percent of the penguin range covered by a biodiversity hotspot that is protected).

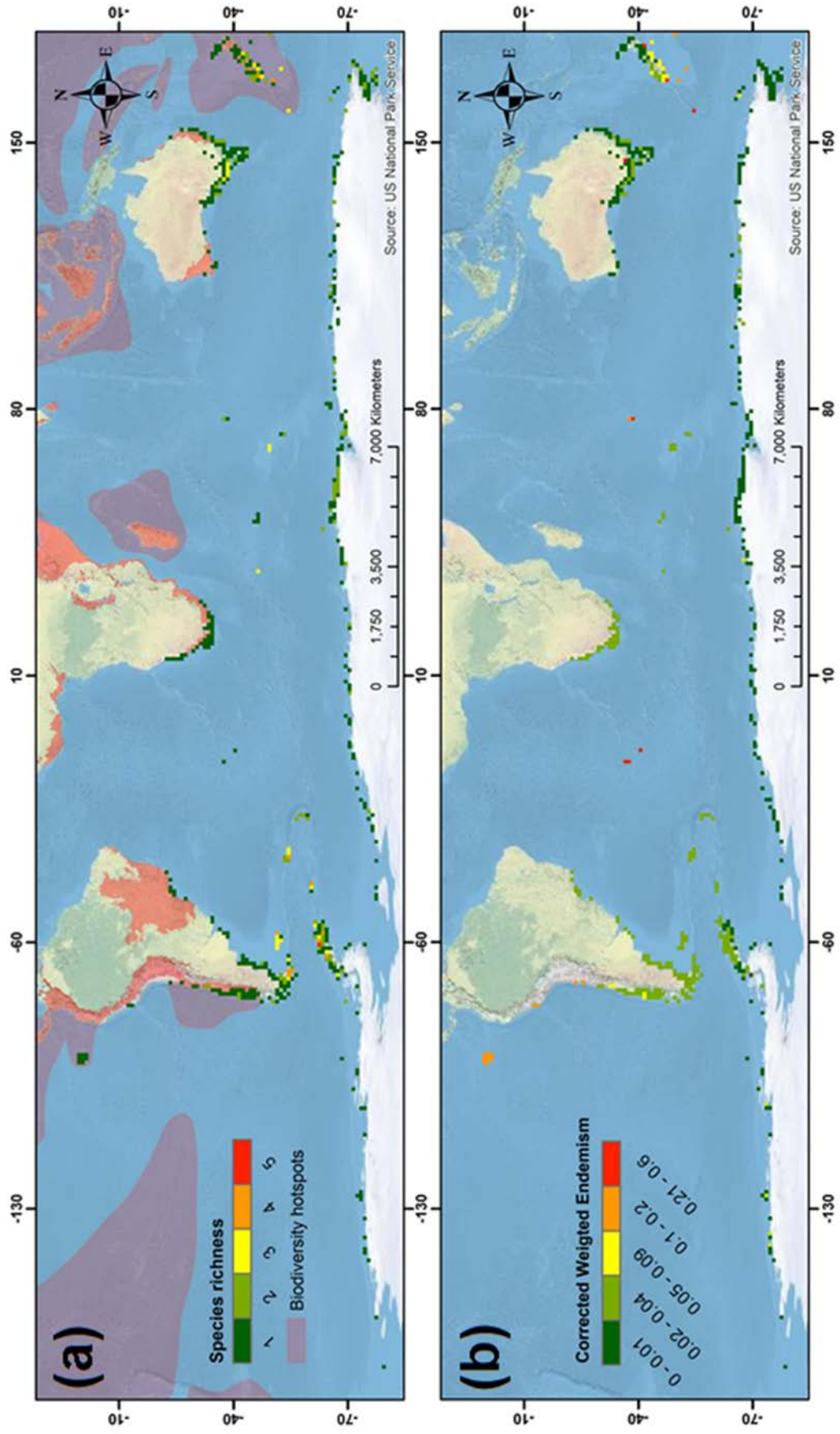


Figure 4: Map of (a) species richness, including biodiversity hotspot coverage, and (b) corrected weighted endemism projected using the World Geodetic System 1984.

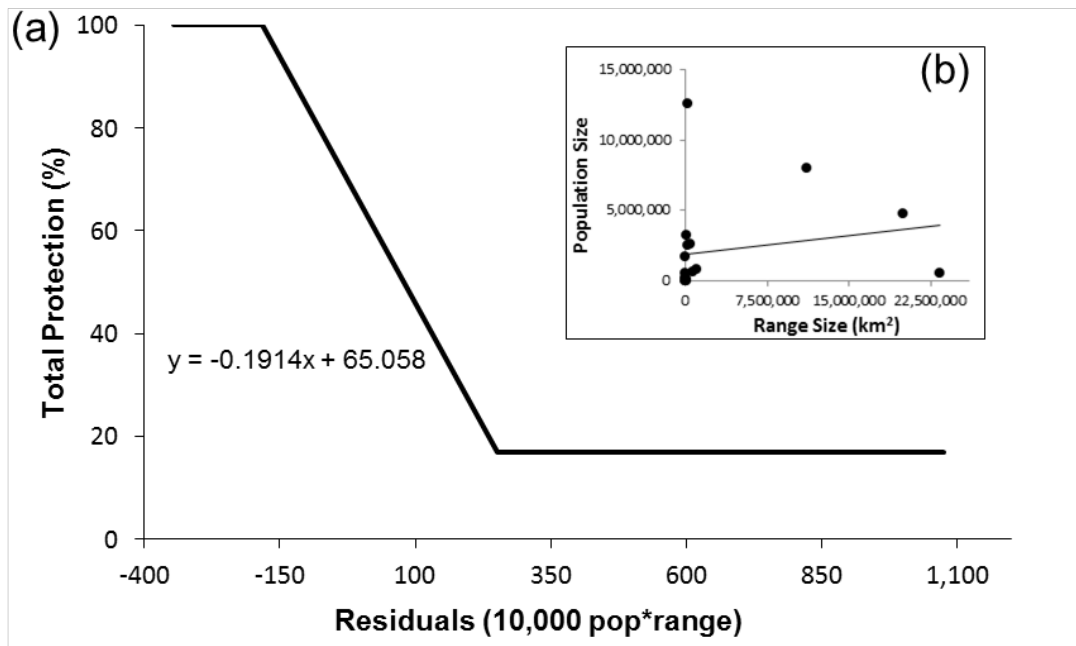


Figure 5: (a) General linear model for species protection target. The residuals from (b) the linear model of population and range size are regressed with the estimated target for total protection: 100% protection, upper limit, for species with residuals in the 10% quantile (species with small populations for their range size); 17% protection, lower limit, for species with residuals in the 90% quantile (species with large populations for their range size). For residuals in other quantiles, targets were interpolated between 17-100%.

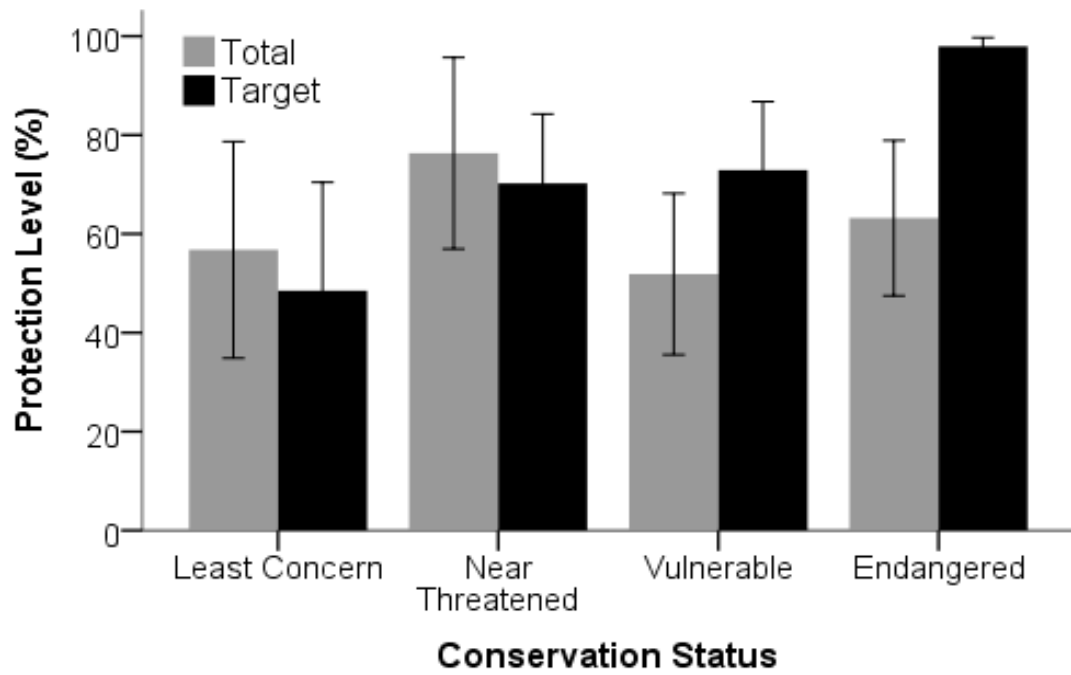


Figure 6: Total and target protection categorized by conservation status. Standard error bars shown.

Supporting Information

Table S1: Number PAs (including all IUCN, NA, and NR categories) within all species ranges. Starred (*) numbers include AT protection, represented as one PA.

Species	Number of PA	IUCN Categories										NA	NR
		Ia	Ib	II	III	IV	V	VI					
<i>E. robustus</i>	1	0	0	0	0	0	0	0	0	0	0	1	0
<i>E. schlegeli</i>	3	1	0	0	0	0	0	0	0	0	0	2	0
<i>E. moseleyi</i>	5	1	0	0	0	0	0	0	0	0	0	3	1
<i>E. sclateri</i>	5	0	0	0	0	0	0	0	0	0	3	1	1
<i>S. mendiculus</i>	5	0	0	1	0	0	0	0	0	0	1	3	0
<i>A. forsteri</i>	29*	22	0	0	0	0	0	0	0	0	0	0	6
<i>P. antarcticus</i>	36*	15	0	2	0	0	0	0	0	0	1	0	17
<i>P. papua</i>	47*	12	0	5	1	9	0	0	3	6	10		
<i>S. humboldti</i>	49	0	0	5	4	20	0	0	10	6	4		
<i>P. adeliae</i>	50*	29	0	0	0	0	0	0	1	0	19		
<i>E. chrysolophus</i>	51	12	0	6	1	10	0	3	8	11			
<i>A. patagonicus</i>	56*	5	0	6	17	10	0	4	9	4			
<i>S. magellanicus</i>	260	20	0	52	6	57	41	16	19	49			
<i>M. antipodes</i>	308	12	0	1	246	6	3	1	1	38			
<i>S. demersus</i>	390	2	2	21	0	44	2	1	14	304			
<i>E. chrysocome</i>	586	79	0	31	48	221	46	130	19	12			
<i>E. pachyrhynchus</i>	1389	141	17	89	805	130	13	78	14	102			
<i>E. minor</i>	5297	420	21	192	3489	324	118	264	37	432			
TOTAL	8567	771	40	411	4617	831	223	516	143	1010			

Table S2: Data for PA and biodiversity hotspot (HS) coverage across all global penguin species.

Species	IUCN*	% IUCN	NC*	% NC	Total*	% Total	None*	% None	Overlap *	% Overlap	HS*	% HS	HS protect- ion*	HS protect- ion
<i>A. forsteri</i>	7.18	0.03	23336.71	100.00	23336.71	100.00	0.00	0.00	7.18	0.03	0.00	0.00	0.00	0.00
<i>A. patagonicus</i>	18.99	20.04	23.27	24.55	39.39	41.56	55.38	58.44	2.87	3.03	5.36	5.66	4.98	5.25
<i>E. chrysocome</i>	12.82	5.82	30.19	13.72	39.51	17.95	180.64	82.05	3.50	1.59	2.12	0.97	2.12	0.97
<i>E. chrysolophus</i>	20.42	8.48	82.27	34.17	98.97	41.11	141.77	58.89	3.73	1.55	0.00	0.00	0.00	0.00
<i>E. moseleyi</i>	0.01	2.08	0.25	61.73	0.25	61.73	0.15	38.27	0.01	2.08	0.00	0.00	0.00	0.00
<i>E. pachyrhynchus</i>	31.98	29.00	46.86	42.49	50.34	45.65	59.93	54.35	28.50	25.84	72.11	65.40	38.67	35.07
<i>E. robustus</i>	0.00	0.00	0.01	100.00	0.01	100.00	0.00	0.00	0.00	0.00	0.01	100.00	0.01	100.00
<i>E. schlegeli</i>	0.38	100.00	0.38	100.00	0.38	100.00	0.00	0.00	0.38	100.00	0.38	100.00	0.38	100.00
<i>E. sclateri</i>	0.33	19.72	1.70	100.00	1.70	100.00	0.00	0.00	0.33	19.72	1.70	100.00	1.70	100.00
<i>E. minor</i>	67.57	10.13	179.18	26.87	191.89	28.78	474.88	71.22	54.86	8.23	524.99	78.74	151.76	22.76
<i>M. antipodes</i>	4.23	20.49	1.72	8.32	5.65	27.35	15.00	72.65	0.30	1.46	20.65	100.00	5.65	27.35
<i>P. adeliae</i>	12.08	0.06	19931.13	99.98	19934.96	100.00	0.00	0.00	8.25	0.04	0.00	0.00	0.00	0.00
<i>P. antarcticus</i>	11.43	0.10	11089.50	99.91	11099.98	100.00	0.00	0.00	0.96	0.01	0.00	0.00	0.00	0.00
<i>P. papua</i>	16.19	1.57	878.22	85.07	890.99	86.30	141.40	13.70	3.41	0.33	0.00	0.00	0.00	0.00
<i>S. demersus</i>	10.50	11.16	24.15	25.66	27.85	29.59	66.26	70.41	6.80	7.22	86.21	91.61	21.76	23.12
<i>S. humboldti</i>	2.77	5.21	1.78	3.35	3.43	6.48	49.60	93.52	1.11	2.09	34.14	64.38	1.73	3.27
<i>S. magellanicus</i>	50.03	12.17	47.42	11.53	78.09	18.99	333.12	81.01	19.36	4.71	103.27	25.11	25.29	6.15
<i>S. mendiculus</i>	7.62	96.32	7.63	96.40	7.70	97.33	61.27	2.67	7.55	95.40	7.91	100.00	7.70	97.33

* Values have been divided by 1,000 km²

Table S3: Penguin hotspots of biodiversity with four or five breeding species at each location.

Colony Location	Number of Species	Name of Species
Falkland Islands	4	<i>A. patagonicus</i> , <i>P. papua</i> , <i>S. magellanicus</i> , <i>E. chrysocome</i>
Tierra del Fuego	4	<i>A. patagonicus</i> , <i>P. papua</i> , <i>S. magellanicus</i> , <i>E. chrysocome</i>
South Georgia/South Sandwich Islands*†	4	<i>A. patagonicus</i> , <i>P. papua</i> , <i>E. chrysolophus</i> , <i>P. antarcticus</i>
Coronation Island/Laurie Island*	4	<i>P. papua</i> , <i>E. chrysolophus</i> , <i>P. antarcticus</i> , <i>P. adeliae</i>
South Shetland Islands*	5	<i>P. papua</i> , <i>E. chrysolophus</i> , <i>P. antarcticus</i> , <i>P. adeliae</i> , <i>A. forsteri</i>
Antarctic Peninsula*	4	<i>P. papua</i> , <i>E. chrysolophus</i> , <i>P. antarcticus</i> , <i>P. adeliae</i>
French Southern and Antarctic Territories (Crozet and Keerguelen) †	4	<i>A. patagonicus</i> , <i>P. papua</i> , <i>E. chrysocome</i> , <i>E. chrysolophus</i>
Auckland Island†	4	<i>P. antarcticus</i> , <i>E. chrysocome</i> , <i>E. sclateri</i> , <i>M. antipodes</i>
Stewart Island†	4	<i>P. antarcticus</i> , <i>E. pachyrhynchus</i> , <i>E. minor</i> , <i>M. antipodes</i>

* Fully protected by the AT

† Fully protected by IUCN/NC PAs

Table S4: Data for the total (sum of IUCN and NC) and target protection levels (calculated using the target model) across all global penguin species and their difference (Total-Target).

Species	Total %	Total (km ²)	Target %	Target (km ²)	Difference (km ²)
<i>S. humboldti</i>	6.48	3434.26	100.00	53032.30	-49598.04
<i>E. chrysocome</i>	17.95	39505.44	52.74	116101.91	-76596.47
<i>S. magellanicus</i>	18.99	78085.58	50.28	206768.74	-128683.17
<i>M. antaripodes</i>	27.35	5647.96	100.00	20650.29	-15002.33
<i>E. minor</i>	28.78	191887.52	90.74	605041.87	-413154.35
<i>S. demersus</i>	29.59	27850.72	100.00	94107.18	-66256.47
<i>E. chrysolophus</i>	41.11	98965.58	17.00	40925.50	58040.08
<i>A. patagonicus</i>	41.56	39387.80	37.71	35741.16	3646.65
<i>E. pachyrhynchus</i>	45.65	50337.37	100.00	110270.94	-59933.56
<i>E. moseleyi</i>	61.73	249.73	90.94	367.93	-118.20
<i>P. papua</i>	86.30	890993.18	87.92	907685.15	-16691.97
<i>S. mendiculus</i>	97.33	7700.67	100.00	7912.10	-211.43
<i>A. forsteri</i>	100.00	23336709.09	100.00	23336709.09	0.00
<i>E. robustus</i>	100.00	7.64	100.00	7.64	0.00
<i>E. schlegeli</i>	100.00	381.24	67.54	257.51	123.74
<i>E. sclateri</i>	100.00	1695.96	98.75	1674.71	21.26
<i>P. adeliae</i>	100.00	19934963.43	42.61	8493380.47	11441582.95
<i>P. antarcticus</i>	100.00	11099976.08	17.00	1886995.93	9212980.15
AVERAGE	61.27	3100432.18	75.18	1995423.91	1105008.27

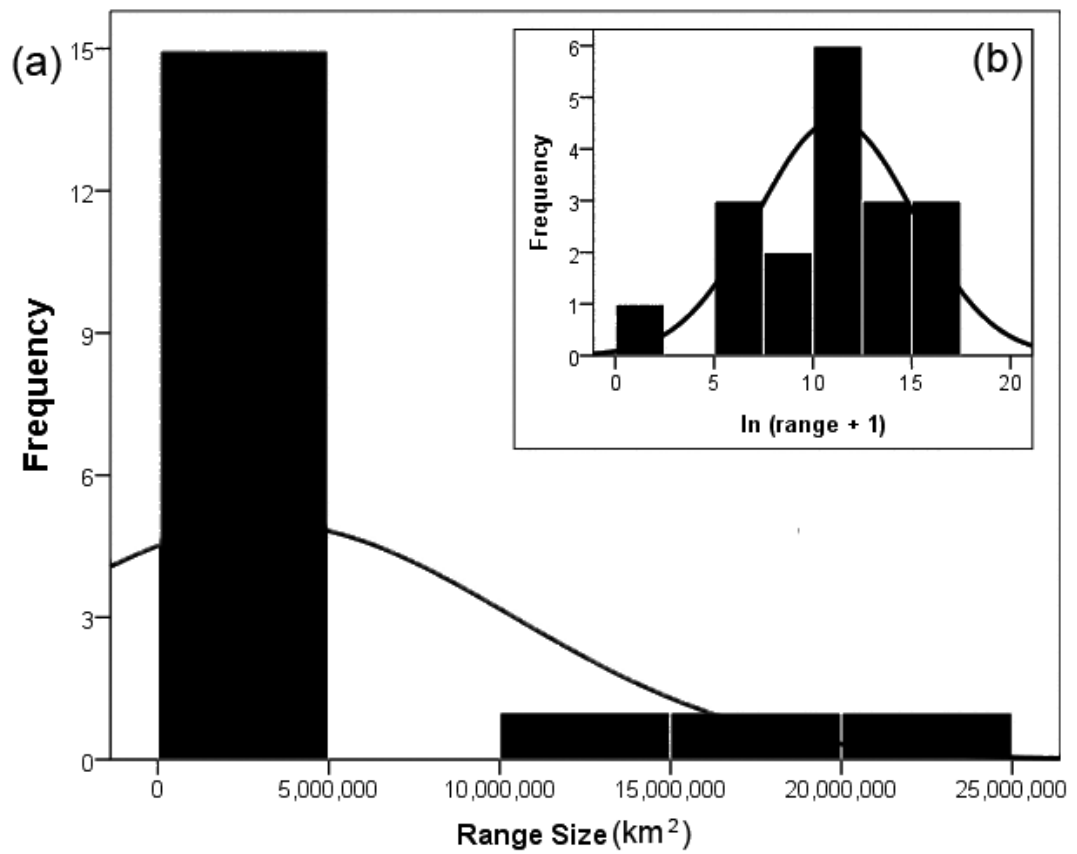


Figure S1: Frequency distribution of (a) the variation in geographic range sizes ($n = 18$) and (b) the same data in their logarithmic scale.

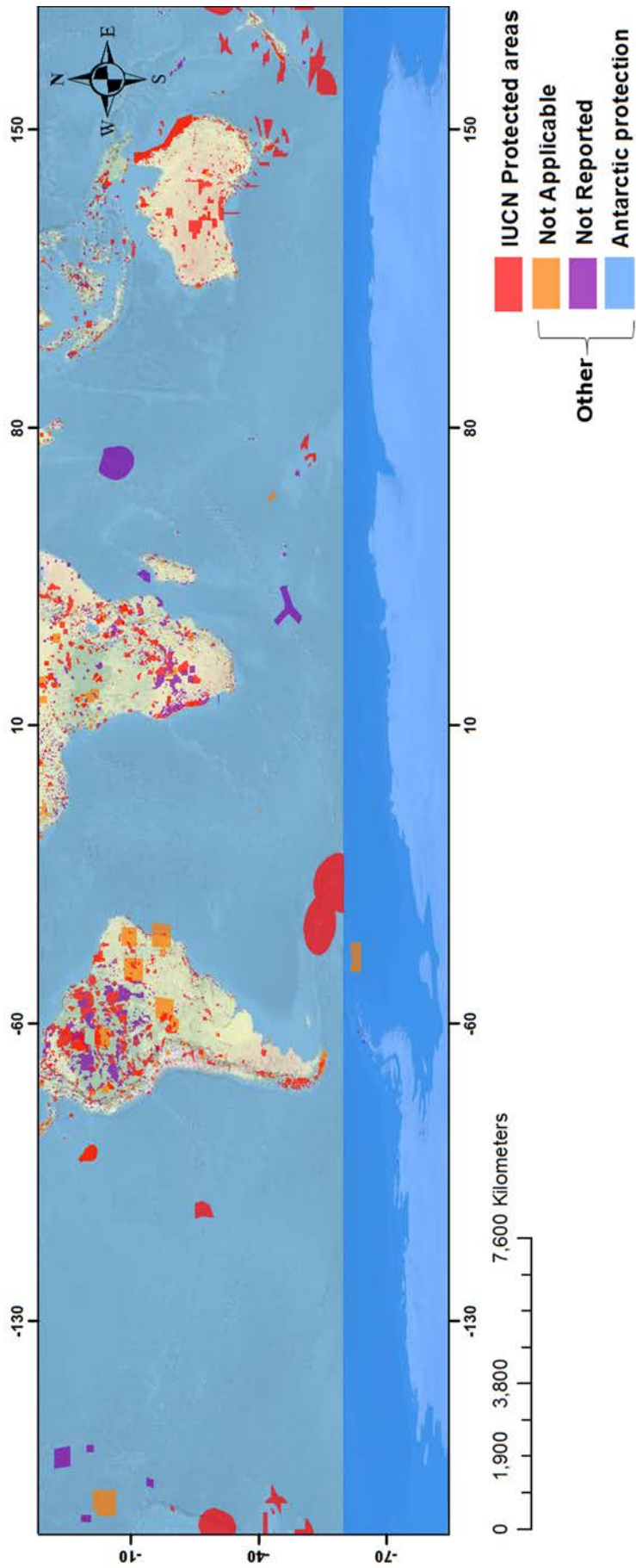


Figure S2: Global PA distribution map, projected using the World Geodetic System 1984.

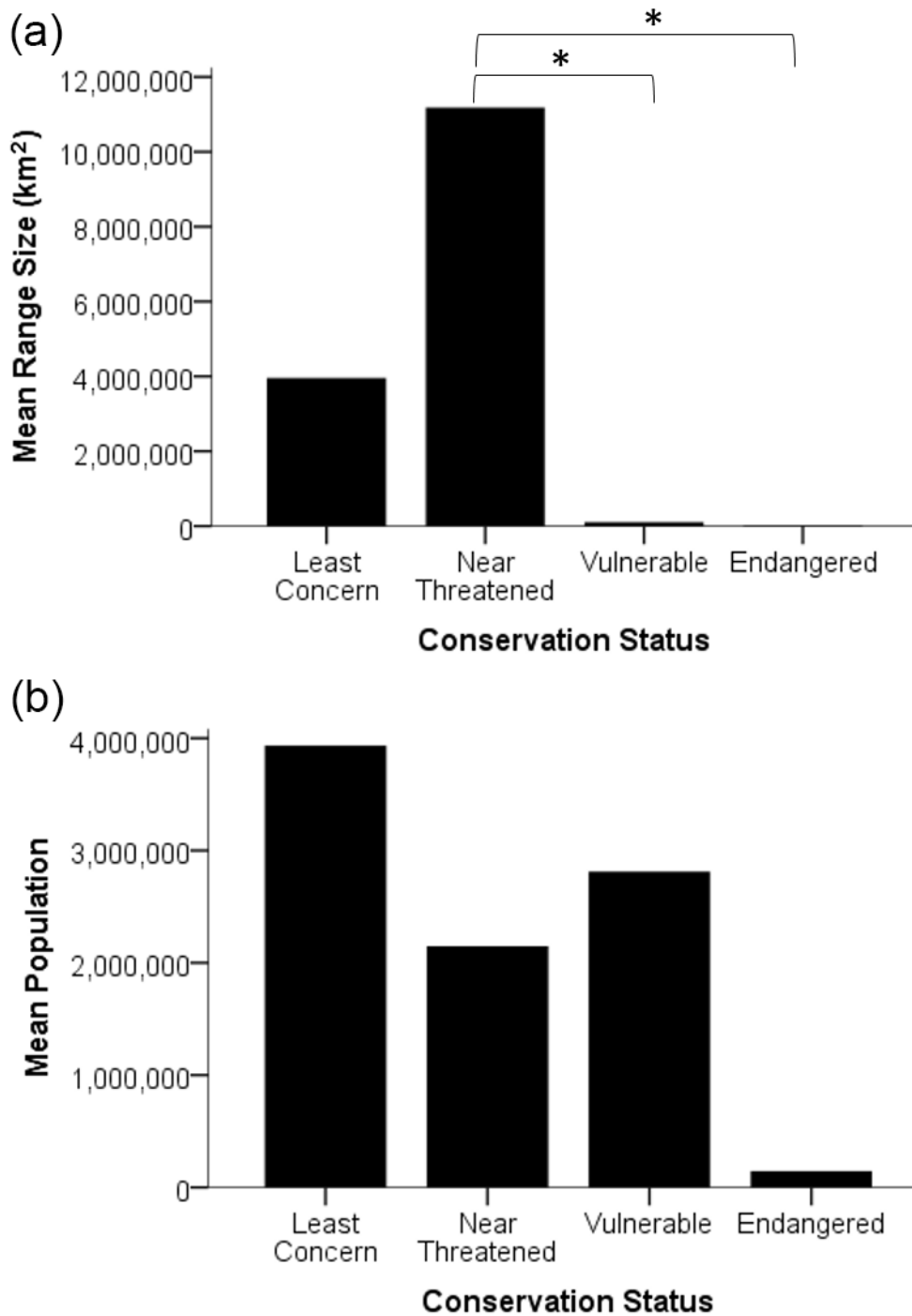


Figure S3: Variation between conservation status and (a) range size (Kruskal Wallis, $X^2 = 11.16$, $n = 3$, $P = 0.01$) and (b) population (Kruskal Wallis, $X^2 = 7.07$, $n = 3$, $P = 0.07$) across all global penguin species to determine if status is influenced by range and population size. A post hoc Tukey's HSD test showed significance only in the range size/status comparison between two variables ($P < 0.05$ denoted with *). Range and population size data are transformed ($\ln+1$) for statistical analyses.

Part 2: Appendices

I have collaborated on three additional research projects, one which is currently in review (Appendix 1) and two which are in preparation for journal publication (Appendices 3 and 4), and therefore include the abstract and figures as a summary.

Appendix 1 presents the analyses of precloacal gland loss in the South American *Liolaemus* lizard radiation. We investigated if gland loss is associated with climatic factors that may have created selection against these structures. Appendix 2 presents the geographic and environmental global distribution patterns, based on niche invasions, of the invasive frog species *Xenopus laevis*. Due to the mechanisms of niche filling and adaptation, *Xenopus* is an example of evolution in action, aided primarily by anthropogenic activities. Appendix 3 summarizes the environmental and anthropogenic factors that determine the evolution of small, intermediate, and large range sizes of *Liolaemus* lizards.

Appendix 1

Evolutionary loss of precloacal signalling glands in a lizard radiation: do multivariate climatic factors hold the key?

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Abstract

Chemical signals play central roles in sexual and ecological communication among animals. In lizards, prevalent mechanisms of sexual communication such as female mate choice have rarely been shown to be influenced by quantitative phenotypic traits (e.g., ornaments). In contrast, chemical signals have been found to influence all major forms of sexual interactions. Chemical signals in lizards are secreted by glands generally located on the edge of the cloaca and the thighs. In the prolific *Liolaemus* lizard radiation from South America, the presence of precloacal glands is common to males of the great majority of species. However, a number of species lack these glands, and existing phylogenetic data suggest that loss of such glands is a secondary evolutionary transition that has taken place in at least a few different clades. Why precloacal glands have been lost multiple times remains a mystery. Here, we investigate whether *Liolaemus* precloacal gland loss is associated with climatic factors that may have created selection against these structures. We show that latitude is the only factor that predicts some differences in species varying in the number of precloacal glands, although this or other factors cannot explain the lack of glands. We suggest that information on species social dynamics (i.e., mating systems) can be an essential factor to elaborate more precise predictions about variation and loss of signalling glands.

Appendix 2

Rapid niche evolution in a globally expanding vertebrate species: large-scale adaptive radiation in the Anthropocene

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Abstract

The evolution of phylogenetic and ecological biodiversity is the result of adaptive radiation following species expansions into novel ecological domains. Therefore, this process has consolidated as one of the central principles in modern evolutionary biology. Given that diversification via adaptive radiation takes long-periods of time, the unfolding of this process has historically been investigated using inferential (e.g., phylogenetic modelling, performance field experiments) approaches. Here, we propose a novel angle to investigate adaptive radiation in action as it unfolds. Human-facilitated species invasions of non-native regions can often expose the invader populations to extreme novel environments. These dramatic changes in the natural selection regimes they experience will either accelerate their extinction or demand exceptionally rapid adaptation in a period of a few decades. To address this theory, we investigate the evolution of multivariate niche of a well-known invasive species, the African amphibian *Xenopus laevis*. This species has successfully invaded a number of environments in different continents, causing strong negative impacts in the resident amphibian communities. We reveal that this amphibian shows signals of a rapid process of adaptive radiation in only a matter of decades. Our global-scale bioclimatic modelling analyses of the niche of *X. laevis* both in its native African environments and in the areas it has ecologically settled show substantial niche evolution. This first body of evidence suggests a new approach to investigate adaptive radiation in action using invasive species as model systems, and reinforces the impact of human activities on the rapid alteration and evolution of biodiversity.

Appendix 3

The macroecology of geographic range size evolution from the perspective of a lizard adaptive radiation

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Abstract

Geographic ranges are a fundamental component and indicator of species ecology, thus reflecting their evolutionary past and their contemporary interactions with the environment. Geographic ranges also critically influence species stability and extinction risk under environmental change. Recently, an increasing interest has emerged in elucidating the factors underlying large-scale patterns of range size variation in order to predict species responses to climate change. Studies have often assumed that ranges in disparate geographical areas are determined by the same processes. However, specific regions are likely to promote evolution of certain range size classes (e.g., small ranges in topographically complex regions), and hence, different range size classes may be intrinsic features of different environments. Using species distribution modelling on a large-scale dataset, we investigate geographic ranges size variation using one of Earth's most prolific vertebrate radiations (*Liolaemus* lizards). We analyse the environmental and anthropogenic factors that determine the evolution of small, intermediate and large ranges using an information-theoretic modelling approach. Our findings show a substantial skew towards small ranges, although there is no tendency for ranges to decrease with decreasing latitude or elevation. In fact, high Andean elevations harbour the vast majority of small ranges and endemic species, where topographic heterogeneity and precipitation are the most substantially limiting factors on species spatial distributions. In contrast, temperature, seasonality, and productivity are the main mediators of range size for intermediate and large ranges. Our findings reveal that contemporary climate plays a dominant role in determining range size within all size classes, which may critically affect species persistence during continuing environmental change. Under rapid climate warming, small range species will likely be faced with significant barriers to dispersal and unable to persist in their current environments, putting the majority of *Liolaemus* species and hotspots of endemism at critically increased risk of extinction.

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