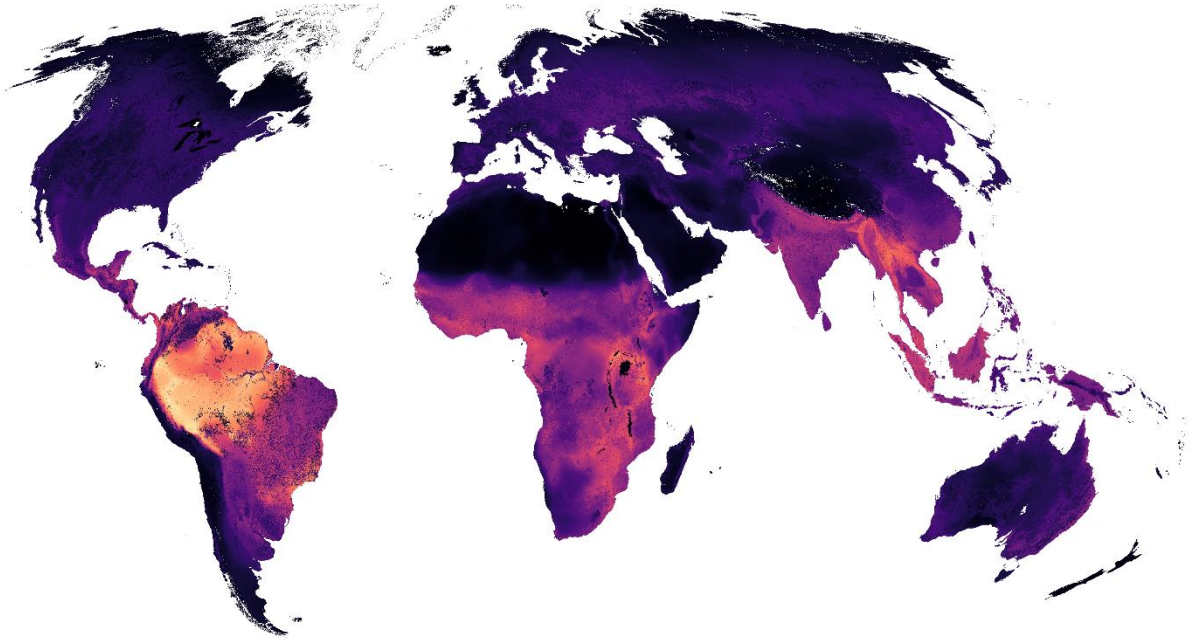
Department of Environmental Biology

PhD in Environmental and Evolutionary Biology

PhD thesis

Where will further Key Biodiversity Areas be identified? A modeling approach to focus efforts



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SUMMARY

Life on Earth is facing a sixth mass extinction, and the main driver of biodiversity loss is habitat destruction. Area-based conservation has been proven vital in preventing species extinction and protecting habitats. However, the current network is not ecologically representative, diminishing the potential role of area-based conservation in reducing biodiversity loss. In this context, identifying new Key Biodiversity Areas (KBAs) is essential. KBAs are defined as 'sites contributing significantly to the global persistence of biodiversity'. Although the KBAs approach is built on previous site-based conservation methodologies, the KBAs identification process still has some challenges to overcome. With this PhD, I aimed to standardize, improve and facilitate the KBAs identification process providing accurate and available biodiversity data for the identification of KBAs and contributing to the KBAs Guidelines for Criterion E, irreplaceability through quantitative analysis.

Area of Habitat (AOH) stands out as a crucial assessment parameter to identify KBAs because it generally reduces the risk of commission error of range maps and is more available than other assessment parameters such as Area of Occupancy (AOO) or the number of mature individuals. AOH is 'the habitat available to a species, that is, habitat within its range'. The production of AOH maps requires an understanding of which habitats a species occurs in. Habitat associations are documented using the IUCN Habitats Classification Scheme. Unvalidated expert opinion is typically used to match habitat to land-cover classes, generating a source of uncertainty in AOH maps. In the first research chapter, *Translating habitat classes to land cover to map Area of Habitat for terrestrial vertebrate*s, I developed a standardised, data-driven methodology to translate IUCN habitat classes into two land-cover maps using point locality data for mammals, birds, amphibians, and reptiles. I generated two translation tables, quantifying the strength of association between habitat and land-cover classes using the odd ratio values of logistic regression models. I calculated the association between habitat and land-cover classes as a continuous variable. However, to map AOH as binary presence or absence, it was necessary to apply an association threshold that can be chosen by the user according to the required balance between omission and commission errors. The data-driven translation provided greater standardisation, objectivity, and repeatability, and the model can be modified for regional examinations and different taxonomic groups.

In the second research chapter, *Mapping Area of Habitat for the world's terrestrial birds and mammals*, I produced an updated version of global AOH maps 5,481 terrestrial mammals and

10,651 terrestrial bird species. For 1,816 bird species defined by BirdLife International as migratory, I developed three AOH maps, one for the resident range, one for the breeding range and one for the non-breeding range. The maps have a resolution of 100 m. On average, AOH covered 66±28% of the range maps for mammals and 64±27% for birds. I used AOH maps to produce global maps of the species richness of mammals, birds, globally threatened mammals and globally threatened birds. These maps represent an increase in resolution compared with species richness maps produced using the IUCN range maps, helping to identify biodiversity hotspots accurately.

Having clear and standardised guidelines to identify KBAs is as crucial for identifying KBAs as having the most accurate high-quality data. The KBAs identification process requires all users to apply the KBAs Standard consistently. However, for KBAs Criterion E, the guidelines are still incomplete as methods are still in development. Sites qualify as Key Biodiversity Areas (KBAs) under KBAs Criterion E if they have a very high irreplaceability value (>0.9 on a 0-1 scale) derived from a quantitative spatial prioritisation analysis. The irreplaceability of a site is determined by both the biodiversity found within it and the biodiversity contained in the other sites considered in the analysis. In the third research chapter, *Evaluating Irreplaceability in KBAs and the effects of the geographical scale*, I explored the identification of KBAs based on Criterion E in two geographical regions, South America and East Africa, for terrestrial mammals. In the South American analysis, I found that, on average, 47% of regionally irreplaceable planning units were not represented in country-level analyses, while country-level analyses mainly represented a subset of the regional ones. These results indicated that at the regional level, irreplaceability was driven by endemic species and species richness, while at the country level, exclusively by endemic species. For some African counties, the analysis produced very few or no highly-irreplaceable planning units. This could indicate that the current targets were too low for these countries. I concluded that the results obtained from the current formulation of Criterion E are affected by the geographical scale and region in which it is applied. The KBAs Standards and Appeals Committee could take some actions to make the analysis more robust, such as setting the scale of application at the regional level and revising the targets. I expect that the research carried out in this PhD constitutes an advance of the current knowledge on KBAs and serve as a starting point for future developments.

CHAPTER 1
GENERAL INTRODUCTION

1.1 State of the art

1.1.1 The global biodiversity crisis

Life on Earth is facing a sixth mass extinction (Barnosky et al. 2011; Pimm et al. 2014; Ceballos et al. 2020). The current rate of species extinctions is at least 100-1000 times higher than background levels (Pimm et al. 2014). Since 1500, at least 338 vertebrate species (77 mammals, 140 birds, 21 reptiles, 34 amphibians, and 66 fishes) have become extinct, and 279 species have become either extinct in the wild or listed as possibly extinct (Ceballos et al. 2015), and these numbers could be much higher as other authors estimated at for birds at least 187 species (Butchart et al. 2018). Of the 29,400 remaining terrestrial vertebrates species, 1.7 % are on the brink of extinction because they have fewer than 1,000 individuals (Ceballos et al. 2020). The rate of decline of vertebrate species population size is 68% form 1970 to 2016 (WWF 2020), 29% of the abundance of the Noth American avifauna has been lost since 1970 (Rosenberg et al. 2019), 82% in flying insect biomass since 1990 (Hallmann et al. 2017). The percentage of threatened animal and plant species is (IUCN 2012a), 25% and this number will increase rapidly if we do not act in the next decade (Díaz et al. 2019a).

We are in the Anthropocene; humans are altering the planet, including geological processes at an incredible rate, we are leaving a pervasive and persistent signature on the planet (Waters et al. 2016). All the limits of planet Earth have been overcome, and several of them have exceeded potential planetary boundaries, including biodiversity loss (Rockström et al. 2009). When a species disappears, a range of characteristics is lost forever, from genes and interactions to phenotypes and behaviours (Ceballos et al., 2020). The disappearance of those can also affect the survival of other endangered species. Mammalian phylogenetic diversity will take millions of years to recover from the current biodiversity crisis even if extinction rates slow (Davis et al., 2018), and the same is likely to be true of other taxonomic groups.

Biodiversity loss is probably the most significant environmental problem humanity faces, extinction is permanent, and all species play a role in the interconnected living system. An

unbalanced living system affects human well-being. Nature's contributions to people are important for our survival and impossible to replace. We need to take action to reduce the intensity of drivers of biodiversity loss. Without action, there will be a further acceleration in the global rate of species extinction (Díaz et al. 2019a). Conservation action prevents extinctions; without it, extinction rates would be 2.9–4.2 times greater than now (Bolam et al. 2020). There is a critical need for immediate efforts to track the drivers and pressures of biodiversity loss.

The five main drivers of biodiversity loss are habitat destruction and degradation, overexploitation, pollution, invasive species and climate change (Secretariat of the Convention on Biological Diversity 2010). The driver with the highest relative impact within terrestrial ecosystems is habitat loss, mainly to land conversion for agricultural lands, pasturelands and plantations (Díaz et al. 2019b). Habitat loss not only affects the local biodiversity where habitat is lost; it also translates into species loss at a regional level in the remaining habitats (Horváth et al., 2019). It is estimated that habitat loss and degradation have reduced terrestrial habitat integrity by 30% relative to background levels, and 9 % of terrestrial species have insufficient habitat to guarantee their long-term survival (IPBES 2019).

Area-based conservation, which includes protected areas and other effective area-based conservation measures (OECMs), has been proven vital in preventing species extinction and protecting habitats (Bolam et al. 2020; Pacifici et al. 2020). However, the current network is not ecologically representative, well-connected, or well-managed, diminishing the potential role of area-based conservation in reducing biodiversity loss (Díaz et al. 2019a). From the IUCN Red List of Threatened Species, 87% have some part of their range covered by protected areas; however only a small minority are adequately represented (Beresford et al. 2011; Butchart et al. 2015; Venter et al. 2018; Maxwell et al. 2020). Protected areas are biased towards locations of low value for other uses and thus do not always capture important areas for biodiversity (Venter et al. 2014; Butchart et al. 2015). In 2010 the world's governments adopted the the Convention of Biological Diversity Aichi Biodiversity Targets, Aichi Target 11, stated that at least 17% of the land areas and 10% of the coastal and marine areas, especially areas of particular importance for biodiversity, should be protected by 2020 (Convention on Biological Diversity, 2010). By 2020, the % coverage element of this target was met (Secretariat of the Convention on Biological Diversity 2020), and in the first draft of the post-2020 global biodiversity framework, the target for the percentage of protected area cover has increased to 30% by 2030, and repeats the recommendation to place them in areas of particular importance for biodiversity.

1.1.2 Key Biodiversity Areas

In this context, identifying new Key Biodiversity Areas (KBAs) is essential (Langhammer et al., 2018). KBAs are defined as sites contributing significantly to the global persistence of biodiversity in terrestrial, freshwater and marine ecosystems (IUCN 2016). KBAs can be used to guide and measure the coverage effectiveness of area-based conservation (Rodrigues, & Cazalis 2020) in the form of protected areas and other effective area-based conservation measures (Donald et al. 2019a), although identifying a KBAs does not imply any form of legal protection. Some authors propose that the post-2020 target on protected areas should focus directly on the cover of KBAs (Visconti et al. 2019). Although some authors argue that it is necessary a prioritization scheme among KBAs to set the necessary management action in each site (Smith et al. 2019) and the it is necessary to be able to measure the effectiveness of each conservation action to set conservation targets

Currently, only 18% of KBAs are entirely covered by protected areas, and 40% are not covered at all (BirdLife International 2021). In this regard, protecting KBAs will clearly improve the representativity of species and their habitats (Hanson et al. 2020a). Independently of the protection level, it is essential to monitor the state of KBAs and the pressures that could affect the biodiversity feature for which each KBAs was identified (Beresford et al. 2020).

The KBAs approach was designed to incorporate and harmonize previous approaches for identifying important sites for biodiversity (IUCN, 2016). KBAs currently comprise Important Bird and Biodiversity Areas (IBAs) identified by Bird-Life International, Alliance for Zero Extinction sites and sites identified through the Critical Ecosystem Partnership Fund hotspot profiles. These new criteria also allowed to overcomes some of the criticisms of previous approaches (Knight et al. 2007) incorporating both threshold and complementary based analysis and establishing the active participation of local stakeholders (Pressey et al. 2021).

The criteria for identifying KBAs are defined in the *Global Standard for the Identification of Key Biodiversity Areas* (KBAs Standard) (IUCN 2016). This document establishes criteria, thresholds and delineation procedures for KBAs identification, in an attempt to harmonise and standardise the existing approaches for identifying important sites for biodiversity. The KBAs approach is built on previous area-based conservation methodologies such as Important Bird and Biodiversity Areas (IBAs) (BirdLife International 2014; Donald et al. 2019b) and Alliance for Zero Extinction sites (AZE) (Ricketts et al. 2005; Parr et al. 2009). The KBAs Standard provided the first umbrella approach designed to apply to all macroscopic species and ecosystems while ensuring that

identification is objective, transparent and rigorous. Currently, around 16,400 KBAs have been identified, and the process is ongoing (BirdLife International 2021).

Sites qualify as a KBA if they meet one or more of five criteria (A-E). Sites qualifying under Criterion A hold a significant proportion of the global population size of threatened biodiversity, including (A1) threatened species and (A2) threatened ecosystems, based on the IUCN Red List for species and ecosystems. Sites qualifying under Criterion B hold a significant proportion of global population size of geographically restricted (B1) individual species (B2) co-occurring species or (B3) assemblages. Sites qualifying under Criterion C hold wholly intact ecological communities. Sites qualifying under Criterion D hold a significant proportion of the global population of a species during (D1) one or more life-history stages, (D2) periods of environmental stress, or (D3) places where the species is produced. Sites qualifying as KBAs under Criterion E have very high irreplaceability identified through a complementarity-based quantitative analysis.

1.1.3 KBAs Assessment parameters: how KBAs are identified

The data unit for several of the KBAs criteria and thresholds is population size, understood to represent the total global number of mature individuals of the species. In principle, the number of mature individuals provides the best (most direct) measure of the proportion of the global population size held by a site; however, such information is unknown for most species. The KBAs Standard therefore provides a range of other assessment parameters that can be used to estimate the proportion of a species' global population size at a site. These include the Area of Occupancy (AOO), the Area of Habitat (AOH), the range, or the number of localities.

Data availability, quality, and bias are common challenges for biodiversity conservation (Meyer et al., 2015; Rondinini et al., 2006), affecting KBAs identification. KBAs identification should be based on the most comprehensive and up-to-date data available and the best available methods for quantitative analysis (KBAs Standards and Appeals Committee 2020). However, accurate, high-quality spatial data is only available for a limited number of species (Rondinini et al. 2005; Rondinini & Boitani 2013) and differs significantly among taxonomic groups and ecosystems.

Area-based assessment parameters (AOO, AOH and range) are available for many more species than are estimates of the number of individuals. Range is defined as the known limits of a species' distribution (IUCN 2018), AOH as the area of habitat available to a species within its range (Brooks et al. 2019) and AOO as the area within the range that is actually occupied (IUCN 2012a). AOO,

by definition, is the most precise of the three metrics, however all three metrics may contain both commission and omission errors (Rondinini et al. 2006). Moreover, AOO is only available for a few species: of the 68% of mammals, birds, amphibians, chondrichthyans, conifers, and cycads assessed under Criterion B, only 15% use AOO as an assessment parameter (Brooks et al. 2019). When AOO is not available, the KBAs Guidelines encourage users to use AOH instead of the range. AOH aims to reduce commission errors of the ranges without incorporating omission errors (see next section). AOH maps have been produced for birds, mammals and amphibians, among entire taxonomic groups (Beresford et al. 2011; Rondinini et al. 2011; Ficetola et al. 2015).

1.1.4 Mapping Habitat to Improve Area of Habitat maps

The most comprehensive and widely used global distribution dataset for mammals and birds is the set of range maps compiled as part of the IUCN Red List of Threatened Species assessments, and they are updated regularly. The IUCN Red List has comprehensively assessed more than 134,400 species and species groups, including mammals, amphibians and birds. The IUCN range maps are generally drawn to minimise errors of omission (i.e. false absence), with the result is that they often contain substantial areas that are not occupied by the species, and so contain errors of commission (i.e. false presence) (Ficetola et al. 2014; Di Marco et al. 2017b). Area of habitat is the 'habitat available to a species, that is, habitat within its range' (Brooks et al., 2019). Consequently, the production of AOH maps requires an understanding of which habitats a species occurs in and where those habitats are located within its broad distribution range (Rondinini & Boitani, 2013).

Habitat is a complex multidimensional concept that does not have a rigorous definition (Kearney 2006). Therefore multiple ways exist to define and quantify habitat (Fischer et al. 2004). IUCN uses a broad definition of habitat considering biogeography, latitudinal zonation and depth in marine systems. Information on habitat is documented for each species assessed following the IUCN Habitats Classification Scheme (IUCN habitat) (IUCN, 2012), a classification and coding system of habitats that ensures global consistency among assessed species. The habitats are defined independently of taxonomy or geography. However, IUCN habitat classes are not spatially explicit, although attempts have recently been made to delimit them (Jung et al. 2020). Land-cover classes derived from remote sensing have been used widely as a surrogate of habitat (e.g. Buchanan et al. 2008; Beresford et al. 2011; Rondinini et al. 2011; Tomaselli et al. 2013; Montesino Pouzols et al. 2014; Corbane et al. 2015; Santini et al. 2019). However, habitat is difficult to interpret in terms of land-cover classes.

A table that translates habitat into land-cover classes is typically used to represent IUCN habitat classes and produce AOH maps spatially. Previous versions have been based on expert knowledge, raising concerns about the accuracy and objectivity of the resulting associations. The assumptions generated in the translation process are rarely considered in detail and the errors are difficult or impossible to quantify (Bradley et al. 2012). Therefore, there is a need for an objective data-driven table to translate habitat classes into land-cover classes (Brooks et al. 2019). Point locality data can be modelled to quantify the power of association between land cover and habitat classes. Data-driven methods can be evaluated and validated quantitatively; therefore, they offer a more rigorous and standardised performance than expert-based opinion (Peterson et al. 2018).

1.1.5 Mapping Area of Habitat

Once Habitat Classification Scheme classes have been converted into land-cover classes, these data can be combined with data on the altitudinal range of a species to derive its AOH. Area of Habitat (AOH) is a type of deductive habitat modelling. Deductive habitat models are not statistical models but methods of using knowledge of species' habitat that seek to increase the resolution (Rondinini et al. 2005; Rondinini & Boitani 2013). Deductive habitat models refine existing range limits and capture habitat loss and fragmentation better than range maps (Ocampo-Peñuela & Pimm 2014).

Previously, AOH was known as Extent of Suitable Habitat (ESH), and different methodologies have been used to determine it. Beresford et al. 2011 produced AOH based on land cover and altitudinal range to redefine EOO and found that AOH covered a mean of 27.6% of the EOO for 157 threatened African bird species. Rondinini et al. (2011) considered elevation, land cover but also hydrological features and tolerance to human process and found that AOH covered on average 55% of range maps for 5330 terrestrial mammal species. Tracewski et al. (2016) evaluated only forest-dependent species with remote sensing forest layers and found that AOH covered 41.2 % of the range.

Brooks et al. 2019 introduced the term Area of Habitat as preferable to the term of Extent of Suitable Habitat, as habitat is, by definition, suitable for the species in question. They also established a standardised methodology to produce AOH maps and framed the concept in the context of the Red List. AOH indicates the parts of the range map that contain land-cover types associated with the habitat preference of the species and that fall inside its altitudinal limits. AOH was defined as a new spatial metric in the Red List different from EOO and AOO (Fig 1.1). AOH cannot be used to evaluate the criteria to determine the extinction risk, although trends in AOH can be used to estimate the rates of population decline under Red List Criterion A. Measuring AOH refined

information about where terrestrial species live, and it is both geographically and taxonomically comparable. Therefore, AOH is critical for area-based conservation and the KBAs identification process.

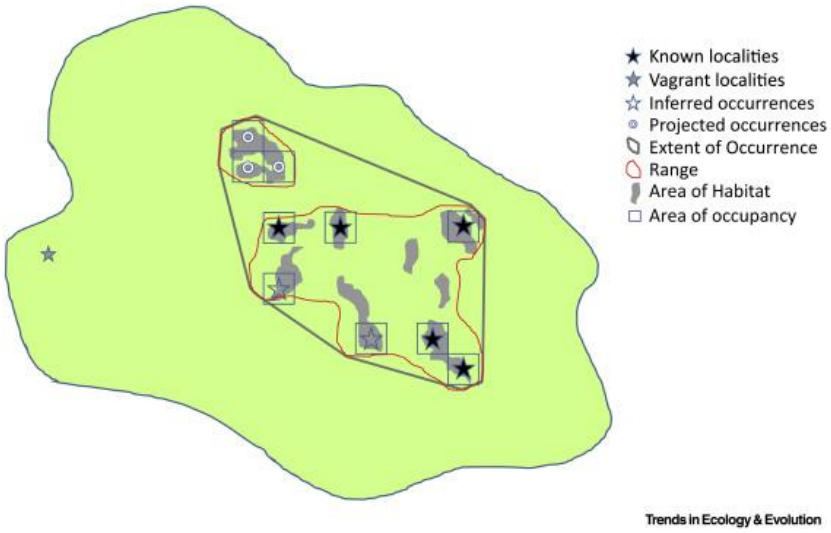

Figure 1.1. Hypothetical Example of the Relationship between Extent of Occurrence, Mapped Range, Area of Habitat, and Area of Occupancy (from Brooks et al. 2019) "Known" sites of occurrences are known localities based on well documented recent. "Vagrant" refers t to sites where the species have been recorded but is not naive. "Inferred" refers to the use of information about habitat characteristics, dispersal capability, rates and effects of habitat destruction and other relevant factors based on known localities to deduce a very high likelihood of presence. "Projected" refers to spatially predicted occurrences based on habitat maps or models. "Extend of occurrence" it the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred, or projected sites of present occurrence of a taxon, excluding cases of vagrancy. "Range" is the current 'limits of distribution of a species, accounting for all known, inferred or projected sites of occurrence. Area of Habitat" (AOH) is habitat available to a species, that is, habitat within its range. "Area of occupancy "is the area which is occupied by a taxon, excluding cases of vagrancy', measured as the occupied cells of a grid with the standard scale of 2×2 kms.

1.1.6 Guidelines on KBAs Criterion E: Irreplaceability

Having clear and standardised guidelines to identify KBAs is as crucial for identifying KBAs as having the most accurate high-quality data. The KBAs identification process requires all users to apply the KBAs Standard consistently. Information on the steps for identifying and delineating

KBAs can be found in the *Guidelines for using A Global Standard for the Identification of Key Biodiversity Areas* (KBAs Standards and Appeals Committee 2019). The KBAs guidelines ensure that the process is based on consistent, scientifically rigorous yet practical methods

However, for KBAs Criterion E, the guidelines are still incomplete as methods are still in development. Criterion E states that sites qualify as KBAs if they have very high irreplaceability values (of ≥0.90 on a 0–1 scale) as identified through a quantitative analysis of irreplaceability. Irreplaceability is defined as either (a) the likelihood that an area will be required as part of a system that achieves a set of targets (Ferrier et al. 2000) or (b) the extent to which the options for achieving a set of targets are reduced if the area is unavailable for conservation (Pressey et al. 1994).

Traditionally, two different approaches have been used in identifying locations to focus on in area-based conservation. The first is a threshold-based approach, which evaluates a set of criteria and associated thresholds to identify sites. This is the case of IBAs, or Criteria A, B and D from the KBAs Standards (Donald et al. 2019b; KBAs Standards and Appeals Committee 2019; Smith et al. 2019). Second, there are complementarity-based approaches, derived from systematic conservation planning (Margules & Pressey 2000). This second approach is incorporated into Criterion E through the concept of irreplaceability. However, irreplaceability have not been applied before in the context of Key Biodiversity Areas. (Di Marco et al. 2016; Smith et al. 2019).

Some authors have explored the relationship between these two approaches in the context of KBAs, analysing the levels of surrogacy and complementary between the two approaches. Di Marco et al., (2016) explored the relationship between IBA's and irreplaceability values. They found that inside IBAs, the irreplaceability values were significantly higher than the regional background values, especially for those IBAs triggered by range-restricted species. Smith et al., (2019) encouraged the integration of both approaches using Criterion E in regions where other KBAs criteria have been applied to identifying additional sites with high irreplaceability. Despite these efforts, the two approaches still have two parallel development, and Criterion E is underrepresented/not represented in the KBAs network (Smith et al. 2019). Therefore, it is crucial to establish clear guidelines to apply this Criterion.

1.1.7 The effect of the geographical scale in the calculation of irreplaceability

As irreplaceability is a complementarity-based measure, the irreplaceability of a site (or planning unit) depends on the biodiversity it contains as well as the biodiversity contained in the other sites that are considered in the analysis. Therefore, the geographic scale of the analysis and the set of biodiversity features (e.g., species) analysed influence the irreplaceability patterns and values.

As KBAs are globally significant sites for biodiversity, the contributions of a site for a given biodiversity element should be measured in relation to the global population (for species) or extent (for ecosystems) (IUCN 2016). This presents some challenges, as calculating irreplaceability at a global scale (and at an appropriate resolution for application to sites) requires considerable computing power, and global data may be less accurate than national data for well-studied countries. Moreover, the KBAs Standard specifies that the identification of KBAs must be led at the country level. Therefore, it is necessary to establish mechanisms to calculate irreplaceability at the country level that represent global importance for biodiversity.

1.2 Scope and objectives

KBAs lie at the interface between science and policy. From a conservation science perspective, KBAs represent a repository for biodiversity knowledge, although the network of sites contains important taxonomic and geographical gaps. KBAs host unique species and ecosystems, and their conservation is essential to safeguard life on Earth. The KBAs Standard allows the identification of sites essential for the persistence of biodiversity using rigorous and standardised criteria and thresholds. From a policy perspective, KBAs allow the classification of land to highlight areas that need special attention for the persistence of biodiversity. Moreover, KBAs mobilise knowledge among different stakeholders. The World Database of Key Biodiversity Areas provides an accessible support tool with information derived from experts, academics, scientists, local people, indigenous communities and environmental organisations (BirdLife International 2021).

There is a need to facilitate and improve the KBAs identification process to make it as accessible and comprehensive to stakeholders as possible (Sinclair et al. 2018). Maxwell et al. (2018) identified the main needs and concerns of KBAs Standard end-users stakeholders, including civil society, academia, national and regional government, the private sector, and intergovernmental

agencies. Some of the stakeholder concerns were: the lack of biodiversity data and how this would limit the identification of KBAs, the standardisation of the KBAs identification procedure, and the prioritisation between KBAs and how this affects conservation action. This PhD arises from the need to overcome some of the concerns.

With this PhD, I aimed to improve and facilitate the KBAs identification process, fulfilling two main objectives. The first objective was to provide accurate and available biodiversity data for the identification of KBAs. AOH is a key KBAs assessment parameter. It is more available than other assessment parameters such as AOO and the number of mature individuals, and reduces the commission errors of range maps. AOH is the habitat available inside range maps (Brooks et al. 2019). Habitat information is documented in the IUCN Habitats Classification Scheme (IUCN habitat; IUCN, 2012)), however, IUCN habitat classes are not spatially explicit. Therefore, it is essential to produce an objective and repeatable transaltion table that allows converting habitat to land cover and quantify the uncertainty. This information made it possible to create accurate AOH at a higher resolution than before.

The second objective was to contribute to the KBAs Guidelines for Criterion E. The KBAs identification process is a bottom-up work, and therefore all users must apply the KBAs Standard consistently. The Guidelines for using A Global Standard for the Identification of KBAs ensure that KBAs identification is based on consistent methods and explains how the KBAs criteria and thresholds should be applied in practice. However, this guidance is still missing for Criterion E, irreplaceability. It is essential that Criterion E is tested consistently to inform the guidelines in its applications.

1.3 Structure of the Thesis

The thesis is structured in three chapters that represent the main objectives of the thesis.

Chapter 2: Translating habitat classes to land cover to map Area of Habitat for terrestrial vertebrates

I developed a standardised, data-driven methodology to translate IUCN habitat classes into two land-cover maps, using point locality data for mammals, birds, amphibians, and reptiles. This analysis aimed to develop a translation table quantifying the power of association between land-cover and habitat classes by modelling land-cover class at point localities as a function of the habitat

associations of the species occurring there. This work was used to produce more reliable AOH maps that will be used to identify KBAs.

Chapter 3: Mapping Area of Habitat for the world's terrestrial birds and mammals

I produced an updated version of global AOH maps for all terrestrial mammals and birds. To produce the AOH maps, I used the translation table between IUCN habitat classes and land-cover classes developed in chapter one, the IUCN ranges from 2020 and updated data on elevation ranges. These maps allowed determination of the global distribution of mammals and birds at a finer resolution than can be obtained using ranges. In the KBAs context, AOH is being used as an assessment parameter for KBAs criteria A1, B, and D.

Chapter 4: Evaluating Irreplaceability in KBAs and the effects of the geographical scale

I evaluated the effect of the geographical scale in application of Criterion E. I studied how irreplaceability values and distribution differ between country- and regional-level analysis. Moreover, I characterised the irreplaceable areas at each of these scales. I worked in two study regions with mid-high richness using the AOH map produced in chapter two. The results of this chapter in this chapter will inform the guidelines on KBAs identification.

CHAPTER 2
TRANSLATING HABITAT CLASS TO LAND COVER TO MAP AREA OF HABITAT OF TERRESTRIAL VERTEBRATES

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2.1 Abstract

Area of habitat (AOH) is defined by Brooks et al. (2019) as the "habitat available to a species, that is, habitat within its range" and is produced by subtracting areas of unsuitable land cover and elevation from the range. The International Union for the Conservation of Nature (IUCN) Habitats Classification Scheme provides information on the species habitat associations, and unvalidated expert opinion is typically used to match habitat to land-cover classes, generating a source of uncertainty in AOH maps. We developed a data-driven method to translate IUCN habitat classes to land cover based on point locality data for 6,986 species of terrestrial mammals, birds, amphibians, and reptiles. We extracted the land-cover class at each point locality and matched it to the IUCN habitat class or classes assigned to each species occurring there. Then we modeled each land-cover class as a function of IUCN habitat with logistic regression models. The resulting odds ratios were used to assess the strength of the association between each habitat and land-cover class. We then

compared the performance of our data-driven model with those from a published translation table based on expert knowledge. We calculated the association between habitat classes and land-cover classes as a continuous variable, but to map AOH as binary presence or absence, it was necessary to apply a threshold of association. This threshold can be chosen by the user according to the required balance between omission and commission errors. Some habitats (e.g., forest and desert) were assigned to land-cover classes with more confidence than others (e.g., wetlands and artificial). The data-driven translation model and expert knowledge performed equally well, but the model provided greater standardization, objectivity, and repeatability. Furthermore, our approach allowed greater flexibility in the use of the results and uncertainty to be quantified. Our model can be modified for regional examinations and for different taxonomic groups.

Keywords

commission and omission errors, Copernicus Global Land Service Land Cover (CGLS-LC100), ESA Climate Change Initiative (ESA-CCI), IUCN Habitat Classification Scheme, IUCN Red List, habitat suitability models

2.2 Introduction

Because habitat loss is the most important driver of biodiversity decline (Díaz et al. 2019a), there is an urgent need to determine where habitat is located within each species' distribution (Pimm et al. 2014; Brooks et al. 2019). Several approaches have been developed to map global species' distributions, but accurate spatial data are only available for a limited number of species (Rondinini et al. 2005; Rondinini & Boitani 2013).

The most complete data set of maps of species' ranges is that available in the International Union for Conservation of Nature (IUCN) Red List (www.iucnredlist.org). The IUCN Red List has assessed comprehensively more than 134,400 species and species groups, including mammals, amphibians, and birds. The IUCN range maps are generally drawn to minimise errors of omission (i.e. false absence), with the result that they often contain substantial areas that are not occupied by the species and so contain errors of commission (i.e. false presence) (Ficetola et al. 2014; Di Marco et al. 2017b).

Area of habitat (AOH) (previously known as extent of suitable habitat, or ESH) is the 'habitat available to a species, that is, habitat within its range' (Brooks et al. 2019). Maps of AOH are produced by subtracting unsuitable areas from range maps based on data on each species' associations with land cover and elevation altitude (Beresford et al. 2011; Rondinini et al. 2011;

Ficetola et al. 2015) the aim of which is to reduce commission errors in range maps. Therefore, the production of AOH maps requires an understanding of species' habitat and where such areas are within its range.

Information on habitat preferences is documented for each species assessed on the IUCN Red List (IUCN 2013) following the IUCN Habitats Classification Scheme (IUCN habitat) (IUCN 2012b), a classification and coding system of habitats that ensures global consistency. The habitats are defined independently of taxonomy or geography. However, IUCN habitat classes are not spatially explicit, although attempts have been made to delimit them (Jung et al. 2020). Land-cover classes derived from remote sensing have been used widely as a surrogate of habitat (e.g. Buchanan et al. 2008; Beresford et al. 2011; Rondinini et al. 2011; Tomaselli et al. 2013; Montesino Pouzols et al. 2014; Corbane et al. 2015; Santini et al. 2019), although habitat is a complex multidimensional concept that is difficult to simplify into land-cover classes.

A table that translates habitat into land-cover classes is typically used to represent IUCN habitat classes spatially and to produce AOH maps. Such tables have been based solely on expert knowledge, raising concerns about the accuracy and objectivity of the resulting associations because the assumptions generated in the translation process are rarely considered in detail and the errors are difficult or impossible to quantify (Bradley et al. 2012). Furthermore, there is a lack of standardisation and repeatability in the procedure (Seoane et al. 2005), which is subject to variability in expert opinion (Johnson & Gillingham 2004).

Repositories of point locality data (i.e. locational records in which particular species have been recorded [Rondinini et al. 2006]) primarily from citizen science have been used successfully in habitat suitability models (e.g. Gueta & Carmel, 2016; Bradter et al., 2018; Crawford, Olds, Maerz, & Moore, 2020). The potential, therefore, exists to use such data to develop an objective data-driven table that can be used to translate habitat into land-cover classes by extracting information on land cover from point localities of species with different habitat associations.

We sought to devise an objective, transparent, repeatable, and data-driven method to produce a table that can be used to translate IUCN habitat classes into land cover based on two widely used global land-cover maps, the Copernicus Global Land Service Land Cover (CGLS-LC100) (Buchhorn et al. 2019a) and the European Space Agency Climate Change Initiative land cover 2015 (ESA-CCI) (ESA (European Space Agency) 2017a) and point-locality data for mammals, birds, amphibians, and reptiles (the best-documented groups of species). The aim of this analysis was to

develop a translation table that quantifies the power of association between land cover and habitat classes. In doing so, we aimed to illustrate a method that improves on expert opinion by quantifying errors in associations between habitat and land cover classes and being flexible to the needs of the user in terms of the required trade-off between reducing commission errors and increasing omission errors and that can be developed at different spatial scales, for different taxa, based on any set of habitat or land-cover classes.

2.3 Methods

2.3.1 Data cleaning and preparation

We downloaded point-locality data for mammals (GBIF, 2019; GBIF, 2020), amphibians (GBIF, 2020) and reptiles (GBIF, 2020) from the Global Biodiversity Information Facility (GBIF) and for birds from GBIF (GBIF, 2019; GBIF, 2020) and eBird (eBird Basic Dataset, 2019). The data were restricted to point localities dated from January 2005 to December 2018 for the model building (70% training and 30% test) and from January 2019 to December 2020 for the evaluation of the model. For eBird data, we selected only stationary point localities with a coordinate uncertainty of <30 m. To minimise errors and uncertainties inherent to repositories of point locality data, we included only the most precisely georeferenced points (Rondinini et al. 2006; Meyer 2012) and applied a set of filters following the guidelines of Boitani et al. (2011). The main attributes considered were currentness, spatial accuracy, and spatial coverage (Fig. 2.1). To make it clear where we are referring to explicit classes, we present land-cover class names in quotation marks and IUCN habitat class names in italics.

The habitat class or classes association for each species was extracted from IUCN (2020). The IUCN habitat classes are standardized terms describing the major habitat types in which taxa occur globally. They follow a hierarchical classification of habitat with three levels. The definitions consider land cover, biogeography, latitudinal zonation, and in marine systems, depth. We used level-1 habitat classes for all habitats except for artificial terrestrial, for which we used a modification of level 2 (Appendix S2.1). We subdivided artificial terrestrial into three subclasses because in terms of land cover these are distinct habitat classes that could aggregate different species (Ducatez et al., 2018).

Because the land-cover classes from the two remote sensing products are exclusively terrestrial, we limited the analysis to species coded only to terrestrial habitat classes, thus excluding species

coded to one or more IUCN marine habitats or to caves and subterranean habitas. We also excluded species coded to more than five level-1 habitat classes because habitat generalists are likely to add little information to the habitat-land cover relationship. In contrast, specialist species coded to only one habitat class provide more insight into the relationship between habitat and land cover. For that reason, for each taxonomic class, we randomly subsampled point records from species coded to more than one habitat class to match the number of points of species coded to one habitat and thereby gave equal weight to habitat specialists even when they had fewer points.

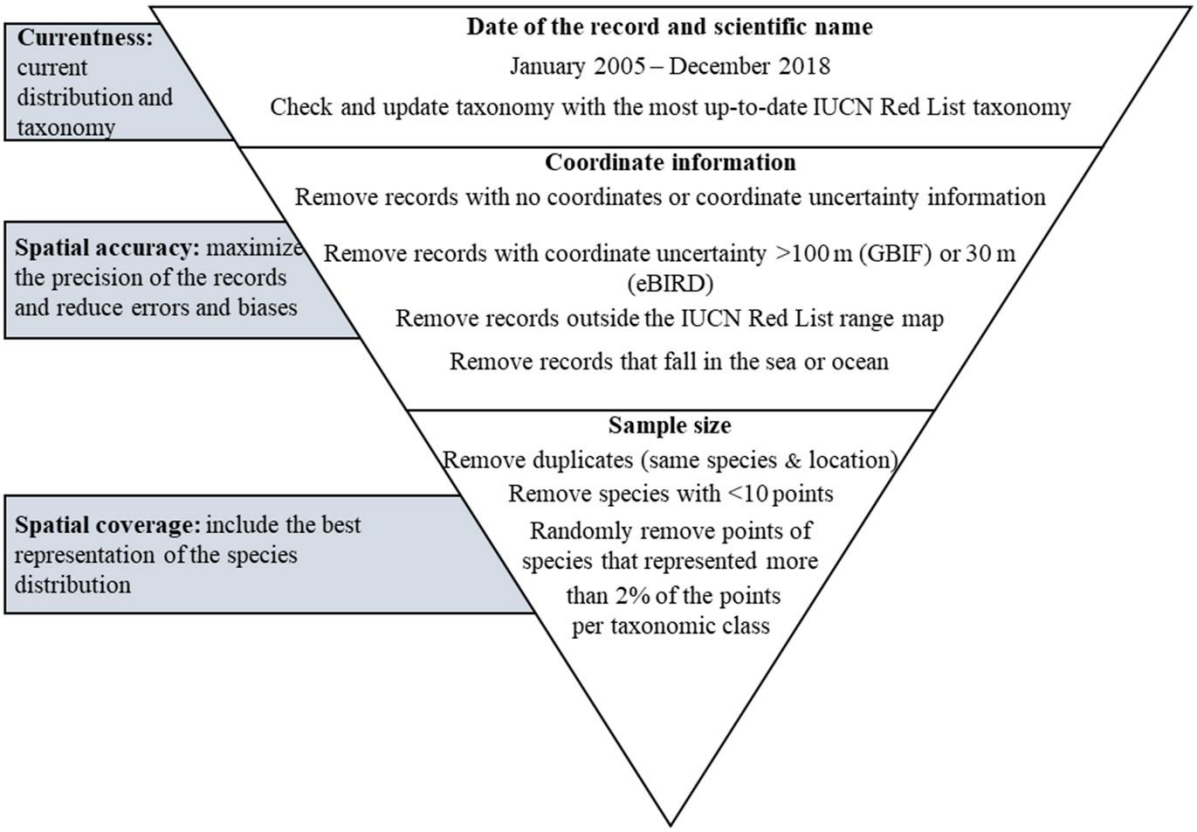

Figure 2.1. Description of the repository point-locality cleaning process, following Boitani et al. (2011). The factors considered are currentness, spatial accuracy, and spatial coverage and are applied from top to bottom (GBIF, 2019; GBIF, 2020, eBird Basic Dataset, 2019).

The two land-cover products used in the analysis have different characteristics. The CGLS-LC100 has a 100-m spatial resolution and a global classification accuracy of 80.2% (Buchhorn et al. 2020). The ESA-CCI has a 300-m spatial resolution and a global classification accuracy of 71.1% (ESA 2017)., although accuracy is dependent on the land cover classes. It is part of a time series from 1992 to 2015, of which we used the 2015 map. Both products use the United Nations Food and Agriculture Organization Land Cover Classification System (UN FAO-LCCS; Di Gregorio & Jansen, 2000), although they have different legends. The CGLS-LC100 has 12 land-cover classes

at level-1 and 23 classes at level-3 (Level-2 is not used by CLGS-LC100); we used level-3. The ESA-CCI has 22 land-cover classes at level-1 and 38 classes at level-2. We used only level-1 because elvel-2 is only available for some regions of the globe.

To prepare the data for the model, we extracted the land-cover class at the coordinates of each point locality. Some land-cover classes did not have enough point localities within them to be modeled, although in all cases these were land-cover classes with very low global coverage. For CGLS-LC100, the underrepresented land-cover classes were "open forest deciduous needle leaf" (10 points, 0.03% of global land surface), "snow and ice" (108 points, 3.1% of global land surface), "moss and lichen" (124 points, 2.3% of global land surface), and "closed forest deciduous needle leaf" (383 points, 3.0% of global land surface). For ESA-CCI, the only class represented too infrequently for analysis was "lichens and mosses" (713 points, 2.2% of global land surface).

2.3.2 Modeling of habitat-land cover associations

To quantify the relationship between IUCN habitat classes and land-cover classes, we modeled the presence or absence of each land-cover class as a function of the IUCN habitat class or classes of the species whose point localities fell within it (Fig. 2.2 and 2.3). An important consideration for modeling was that the number of habitat classes per species varied from one to five. Therefore, it was impossible to model land-cover class as a one-to-one relationship with habitat class because each point location was associated with one or multiple habitat classes. This consideration restricted the number of models we could use for our analysis. We required a flexible model that allowed a many-to-many match between habitat classes and land-cover classes to model this matrix of habitat versus land-cover class relations. In multinomial logistic regression models, the data and the computational power requirements increase exponentially with the number of response categories. In our case, with more than 20 land-cover categories, this option was not feasible. Therefore, we modeled each land-cover class separately, transforming each class into a binary variable of 1 (land cover present) or 0 (land cover not present). Then, we used logistic regressions to model the binary land-cover class variable as a function of the different habitat classes:

$$(1)\quad \log\frac{p_{\mathrm{lc}}}{1-p_{\mathrm{lc}}} = \beta_0 + \beta_1 H_{\mathrm{forest}} + \beta_2 H_{\mathrm{savanna}} + \beta_3 H_{\mathrm{shrubland}} + \beta_4 H_{\mathrm{grassland}} + \beta_5 H_{\mathrm{wetlands}} + \beta_6 H_{\mathrm{rocky\ areas}} + \beta_7 H_{\mathrm{desert}} + \beta_8 H_{\mathrm{artificial1}} + \beta_9 H_{artificial2} + \beta_{10} H_{artificial3} + \beta_{11} H_{artificial4} + \varepsilon$$

where (plc/[1-plc]) is the land-cover odds ratio, βx is the model parameter for the IUCN habitats Hx and ε is the error.

The transformation of the land-cover class into a binary form for each of the models generated a highly unbalanced variable, with many more zeroes than ones. In a logistic regression model, unbalanced data underestimate the probability of an event, so it is recommended that the number of 1s and 0s be adjusted (King & Zeng 2001; Pozzolo et al. 2015). We therefore randomly subsampled the 0s in the training set before running the model. The assumption behind this is that in the majority class there are many redundant observations and randomly removing some of them does not change the estimation of the within-class distribution (Pozzolo et al. 2015).

To reduce the intrinsic spatial and taxonomic bias of point-locality data (Boitani et al. 2011; Meyer et al. 2016) and to account for multiple but varying numbers of point localities per species, we added taxonomic and spatial variables as random effects in the model (Bird et al. 2014). As taxonomic variables, we added species nested within taxonomic class (Amphibia, Reptilia, Aves, Mammalia). Adding intermediate taxonomic groupings (e.g. family or genus) in the nesting would result in many factor levels with single or very few replicates. To test whether there was any bias among taxonomic classes, we produced separate models for each class. This test showed that the association between land-cover and habitat classes from the different translation tables were very similar; therefore, we decided to model all classes together. As a spatial variable, we added the country of the point record as a random effect.

We used the coefficients of the models to evaluate the association between land-cover class and habitat classes. The intercept did not provide any information on the relationship between land-cover class and habitat class because it represented the odds of a point locality falling within a particular land-cover class after the subsampling of the data set, independently of the habitat (Ranganathan et al. 2017). The coefficients represented the odds ratio, in other words, the odds of a point locality falling within a particular land-cover class (when the species to which the point locality relates is coded for a particular habitat class) divided by the odds of the species occurring in that land-cover class when it is not coded for that habitat class. The ratio, therefore, indicates the extent to which being coded to a particular habitat class increases or decreases the odds of a species being found in a particular land-cover class. The units of the logit function are log(odds ratio), but for easier interpretation, we changed them to the exponential and present the results as odds ratios.

Odds ratio values below 1 indicate a negative association between land cover and habitat classes, whereas those above 1 indicate a positive association. Because the odds ratio is a continuous variable, it is necessary to set a threshold to transform the results into a binary translation table that can be used to assign, or not, a particular habitat class to a particular land-cover class. The threshold can be modified according to the needs of the user based on the required balance between minimising commission errors (land-cover classes incorrectly associated with a habitat class) and increasing omission errors (land-cover classes incorrectly omitted from a habitat class). Coefficients that had $p > 0.05$ were considered to indicate a lack of association between land cover and habitat classes. To adjust the significance threshold of the p values for multivariable analysis, we used Bonferroni corrections.

To validate the models, we set aside 30% of the point occurrence data for testing, leaving 70% to train the model. As a validation test, we used the area under the curve (AUC) from a receiver operating characteristic (ROC) curve (Jiménez-Valverde 2012). The AUC is a model accuracy measure that provides information on how well a model can distinguish among classes. In our case, we used it to test how well the models predicted the presence or absence of a point locally in a given land cover class. The AUC values range from 0 to 1; a value of 0.5 meant the model did not perform better than random, whereas a value of 1 indicated the model perfectly separated the two groups.

The results of the models can also be mapped spatially using one of the three thresholds of associations (low, middle, and high tertial) between habitat and land-cover classes. In such maps, habitats are overlaid because the same land-cover class may represent more than one habitat class or because both habitats occur in the same geographical areas. The overlap among habitats increases as the threshold of association is reduced.

We then compared the performance of the data-driven translation table with that of an expert-knowledge translation table (Santini et al. 2019) based on the same ESA-CCI land-cover classification used here. We did not find any published translation table that used CGLS-LC100. Santini et al. (2019) compared the ESA CCI land cover classes with level-2 IUCN habitat classes, so we aggregated the habitat classes to level-1 IUCN habitat classes to make the two translation tables comparable. We limited the comparison to birds and mammals because they were the taxonomic groups considered by Santini et al. (2019). For each species, we mapped habitat based on both tables. We assessed the proportion of points located in the suitable areas (point prevalence) and compared it with the proportion of habitat inside the species' range (model prevalence) to

determine whether the results were better than a randomly assigned set of points (Rondinini et al. 2011). We used a new set of point localities, 211,304 point localities for 489 species of mammal and 461,277 point localities for 2,112 species of bird

2.4 Results

The number of point localities and species available for analysis was 200,683 and 455 respectively for mammals, 4,083,510 and 5,154 for birds, 92,327 and 479 for amphibians, and 131,077 and 898 for reptiles. For the CGLS-LC100 land-cover product, 71 coefficients showed a significantly positive association (odds ratio >1) and 38 coefficients showed a significantly negative association (odds ratio <1) between land-cover classes and habitat classes (Fig. 2.2). For the ESA-CCI land-cover product, 101 coefficients showed a significantly positive association, and 40 coefficients showed a significantly negative association (Fig. 2.3).

Higher odds ratios (>1) indicated stronger positive associations between land-cover and habitat classes, and lower odds ratios (nearer to zero) indicated stronger negative associations. We divided the significantly positive values into tertiles to identify three potential thresholds for creating a table of binary association and nonassociation variables for producing AOH maps: 1.138-1.351, 1.362-1.712 and 1.743-13.720 for CGLS-LC100, and 1.121-1.393, 1.396-1.704 and 1.708-19.148 for ESA-CCI.

Forest and *desert* had the strongest positive associations between land-cover and habitat classes. The *forest* habitat class was associated with almost all the forest and tree cover land-cover classes (CGLS-LC100 average positive odds ratio = 3.8; ESA-CCI average positive odds ratio = 4.0) and with no other land-cover classes. The *desert* habitat class was also strongly associated with particular land-cover classes: "shrubs," "herbaceous vegetation", and "bare/sparse vegetation" in CGLS-LC100 (average positive odds ratio = 4.6) and "shrubland", "grassland", "sparse vegetation (tree, shrub, herbaceous cover < 15%)," and "bare areas" in ESA-CCI (average positive odds ratio = 3.0). *rocky areas* were associated with almost the same land-cover classes as *desert* but had lower odds ratios.

IUCN habitat class / Land-cover class	Number point	Forest	Savanna	Shrubland	Grassland	Wetlands	Rocky areas	Desert	Artificial arable and pasture lands	Artificial degraded forest and plantation	Artificial urban areas and rural gardens	Artificial aquatic	AUC
Shrubs	264166	0.309	1.870	2.683	1.188	-	1.383	4.225	-	0.711	-	-	0.882
Herbaceous vegetation	531007	0.372	1.180	1.622	2.369	1.204	1.506	1.517	1.296	0.880	1.262	-	0.793
Cultivated and managed vegetation agriculture	470123	0.588	1.570	1.395	1.748	1.875	0.687	-	1.743	-	1.330	1.523	0.807
Urban / built up	412978	-	-	1.362	-	1.351	-	-	1.488	1.293	3.183	1.696	0.763
Bare / sparse vegetation	30746	0.139	-	2.026	1.524	-	3.380	8.192	-	0.489	-	-	0.924
Permanent water bodies	112799	0.603	-	-	-	2.189	-	0.698	1.236	-	1.447	1.712	0.745
Herbaceous wetland	87084	0.732	1.240	-	1.248	3.185	0.631	0.367	1.215	1.220	1.396	2.360	0.827
Closed forest, evergreen needle leaf	415369	3.824	0.384	-	0.706	-	-	0.229	0.592	0.530	-	0.674	0.885
Closed forest, deciduous needle leaf	630019	13.720	0.455	0.382	0.475	-	0.483	0.052	0.735	1.516	0.748	-	0.940
Closed forest, deciduous broad leaf	311541	2.520	1.704	-	-	1.560	-	0.174	-	-	1.435	-	0.867
Closed forest, mixed	60555	5.461	0.548	0.671	-	1.523	-	-	-	-	-	-	0.906
Closed forest, unknown	128975	1.971	-	-	-	1.312	-	0.389	-	1.264	-	1.345	0.736
Open forest, evergreen needle leaf	108686	2.171	0.476	-	-	-	1.790	0.578	-	0.454	-	-	0.856
Open forest, evergreen broad leaf	49487	2.442	0.801	-	-	-	0.562	0.160	-	1.566	-	-	0.894
Open forest, deciduous broad leaf	103555	1.391	2.172	-	-	1.658	-	0.251	-	-	1.398	-	0.854
Open forest, mixed	2758	3.038	-	-	-	-	-	-	-	-	-	-	0.899
Open forest, unknown	773407	1.138	1.368	1.284	-	1.302	-	0.673	1.221	1.138	1.167	1.341	0.644

Low positive association (odds ratio = 1.138 - 1.351) **Medium positive association (odds ratio = 1.362 - 1.712)** **High positive association (odds ratio = 1.743 - 13.720)**
Negative association **Non significant association**

Figure 2.2. Odds ratio values describing the association between Copernicus Global Land Service Land Cover (CGLS -LC100) classes and International Union for the Conservation of Nature (IUCN) Habitat Classification Scheme. Odds ratio values < 1 indicate a negative association, and values > 1 indicate a positive association. The positive associations are divided into tertiles (green), indicating 3 possible options for setting a threshold to convert continuous variables into a binary association-nonassociation variable for creating area of habitat maps. AUC indicates the values of Area Under the Curve from a receiver operating characteristic (ROC) curve, a measure of accuracy of a classification mo

IUCN habitat class / Land-cover class	Number point	Forest	Savanna	Shrubland	Grassland	Wetlands	Rocky areas	Desert	Artificial arable and pasture lands	Artificial degraded forest and plantation	Artificial urban areas and rural gardens	Artificial aquatic	AUC
Cropland, rainfed	247928	0.662	1.609	1.417	1.415	1.660	-	-	1.617	1.309	1.393	1.613	0.824
Cropland, rainfed: herbaceous cover	299354	0.732	1.434		1.674	1.581	-	-	1.922	-	1.453	1.678	0.821
Cropland, rainfed: tree or shrub cover	13384	-	-	-	-	-	-	0.354	-	1.613	-	-	0.960
Cropland irrigated or post-flooding	40194	-	-	-	1.704	1.996	-	-	1.763	1.396	1.357	1.708	0.954
Mosaic cropland (>50%) /natural vegetation (tree, shrub, herbaceous cover)(<50%)	122990	-	1.183	1.234	1.253	1.363	-	0.750	1.475	1.283	1.232	-	0.773
Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%)/cropland (<50%)	181508	1.281	-	1.121	1.163	1.326	-	0.609	1.249	1.222	1.202	-	0.709
Tree cover, broadleaved, evergreen, closed to open (>15%)	744491	12.230	0.495	0.354	0.505	0.734	0.391	0.036	0.686	1.354	-	-	0.949
Tree cover, broadleaved, deciduous, closed to open (>15%)	294126	2.016	1.477	1.564	-	1.496	-	0.294	-	0.813	1.451	-	0.834
Tree cover, needleleaved, evergreen, closed to open (>15%)	444643	3.695	0.250	-	-	-	2.011	0.643	0.704	0.431	-	-	0.886
Tree cover, needleleaved, deciduous, closed to open (>15%)	20580	-	-	-	-	1.960	-	-	-	-	-	-	0.868
Tree cover, mixed leaf type (broadleaved and needleleaved)	88806	5.990	0.520	0.705	-	1.510	-	0.463	-	-	-	-	0.898
Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	170385	1.217	-	1.294	-	1.318	-	0.429	1.152	-	1.285	-	0.724
Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	20667	0.788	1.543	1.232	1.675	-	-	-	-	-	-	-	0.874
Shrubland	471187	0.535	1.758	2.133	1.309	-	1.678	1.603	-	0.702	-	0.626	0.873
Grassland	323351	0.468	1.469	1.612	2.132	1.348	1.928	1.280	1.281	0.700	1.240	1.453	0.806
Lichens and mosses	778	-	-	-	19.148	-	-	-	-	-	-	-	0.972
Sparse vegetation (tree, shrub,herbaceous cover)(<15%)	80470	0.111	1.547	2.073	2.205	-	1.770	3.919	-	0.449	-	-	0.937
Tree cover, flooded, fresh or brakish water	33641	1.824	-	0.622	0.660	2.793	-	-	-	-	-	2.109	0.886
Tree cover, flooded, saline water	28755	-	-	-	-	2.021	-	0.292	-	1.374	-	1.733	0.888
Shrub or herbaceous cover, flooded, fresh/ saline/brakish water	75650	0.649	1.430	1.191	-	2.585	0.636	-	1.242	-	-	1.990	0.802
Urban area	575679	-	-	1.352	-	1.611	-	0.676	1.755	1.409	3.582	1.718	0.768
Bare areas	33857	0.174	-	2.147	1.457	-	2.717	5.375	-	0.558	-	-	0.877
Water bodies	217197	0.651	-	-	-	2.167	-	0.487	1.221	-	1.598	1.939	0.749

Low positive association (odds ratio = 1.121 - 1.393) **Medium positive association (odds ratio = 1.396 - 1.704)** **High positive association (odds ratio = 1.708 - 19.148)**
Negative association **Non significant association**

Figure 2.3. Odds ratio values describing the association between European Space Agency Climate Change Initiative land cover 2015 (ESA-CCI) classes and International Union for the Conservation of Nature (IUCN) Habitat Classification Scheme. Odds ratio values < 1 indicate a negative association, and values > 1 indicate a positive association. The positive associations are divided into tertiles (green), indicating 3 possible options for setting a threshold to convert continuous variables into a binary association-nonassociation variable for creating area of habitat maps. AUC indicates the values of Area Under the Curve from a receiver operating characteristic (ROC) curve, a measure of accuracy of a classification mode.

Savanna, *shrubland*, and g*rassland* habitat classes were associated with "shrubs", "herbaceous vegetation," and "cultivated and managed vegetation agriculture" in CGLS-LC100 land cover and "cropland", "herbaceous cover", "shrubland", "grassland", "sparse vegetation", "mosaic cropland," and "mosaic herbaceous cover" in ESA-CCI. However, the power of association varied between these different combinations. The *savanna* habitat class was also associated with some forest classes, while *shrubland* and *grassland* habitats were also associated with bare areas.

We divided artificial terrestrial habitats into three different classes: *artificial arable and pasture lands*, *artificial degraded forest and plantations*, and *artificial urban and rural gardens*. These classes had the least certain relationships because the odds ratio values were the closest to 1 (CGLS-LC100 average positive odds ratio = 1.367, 1.333, and 1.577 respectively; ESA-CCI average positive odds ratio = 1.468, 1.370, and 1.579 respectively). Some unexpected land-cover classes were associated with these habitat classes; for example, *Arable and pasture lands* and *degraded forest and plantations* were associated with "urban areas". However, these unexpected associations disappeared when the threshold increased.

Wetland and *artificial aquatic* habitats had intermediate odds ratio values (CGLS-LC100 average positive odds ratio = 1.7; ESA-CCI average positive odds ratio = 1.8). In terms of land-cover associations, they were associated (in some cases strongly) with land-cover classes related to water, but also to some land-cover classes that have no relation with wetlands or aquatic environments (e.g. some type of forest or cultivated areas).

The AUC of models for CGLS-LC100 ranged from 0.644 to 0.940. The land-cover classes with the lowest AUC were the "open and closed unknown forest" (AUC = 0.644 and 0.736) classes, followed by "water bodies" (AUC = 0.745) and "urban areas" (AUC = 0.763). Those with the highest AUC values were the other forest classes (AUC range 0.854 – 0.940) and "bare and sparse vegetation" (AUC = 0.924). For ESA-CCI, the AUC ranged from 0.709 to 0.972. The land-cover classes with the lowest AUC were mosaic land-cover classes (AUC range 0.709 - 0.874), followed by "water bodies" (AUC = 0.750) and "urban areas" (AUC = 0.768). The land-covers with the highest AUC values were “lichens and mosses” (AUC = 0.972), “cropland irrigated or post-flooding” (AUC = 0.954), “sparse vegetation” (AUC = 0.937) and tree cover land classes (AUC range 0.834 – 0.949).

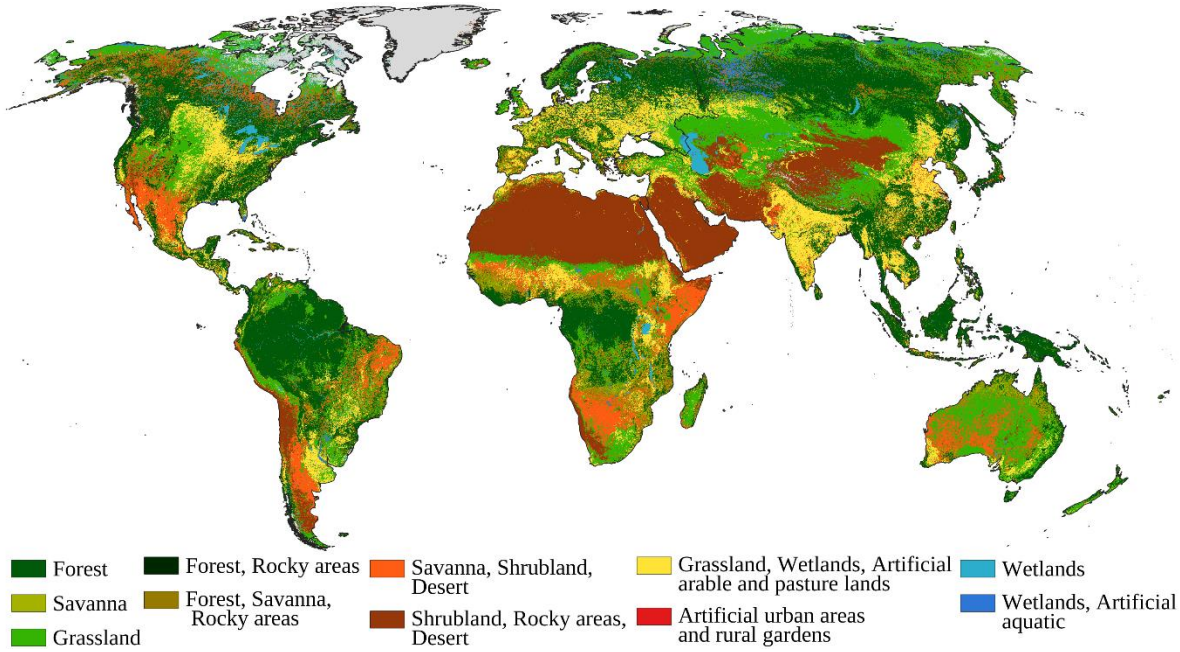

Figure 2.4. Map of habitat classes (level 1) from the International Union for the Conservation of Nature Habitat Classification Scheme based on the highest threshold for Copernicus Global Land Service Land Cover (CGLS -LC100) data-derived translation (Fig 2.2) (Geotiff version Appendix S2).

The spatial representation of the models showed the geographical distribution of the habitat classes (Fig. 2.4, Appendices S2.2 and S2.3). Our analysis show that some habitats had the same geographic distribution. Habitats classes *savanna*, *shrubland*, *desert*, and *rocky areas* had the same geographical extent. In the contrary, forest had their own geographical distribution. *Grassland* had its own distribution and appeared in combination with *artificial arable and pasture and wetlands*.

Point prevalence in Santini et al. (2019) was similar to the point prevalence we found from our model when using the middle and high odds-ratio thresholds (Table 2.1). The ratio between point prevalence and model prevalence (proportion of the range remaining after apparently unsuitable land-cover classes are excluded) between the two methods was also very similar, and higher than 1, indicating that the habitat associations were better than random for both approaches.

Table 2.1 Mean point prevalence[a] and model prevalence[b] for birds and mammals using the three tertile thresholds for ESA CCI land cover derived from data-driven assessment (see Figure 2.4) and the expert knowledge-based assessment of Santini et al. (2019).

Model parameters	*Lower tertile threshold*	*Middle tertile threshold*	*Upper tertile threshold*	*Santini et al. 2019*

Birds				
Point prevalence	0.94	0.81	0.66	0.74
Model prevalence	0.91	0.76	0.59	0.68
Mammals				
Point prevalence	0.93	0.82	0.67	0.73
Model prevalence	0.90	0.80	0.62	0.70

2.5 Discussion

By modeling the relationship between IUCN habitat classes and the CGLS-LC100 and ESA-CCI land-cover classes, we generated two translation tables, quantifying the strength of association between habitat and land-cover classes. Among habitat classes, forest, desert and rocky areas had the strongest associations with land-cover classes, perhaps owing to the higher accuracy of the relevant land-cover classes. For both CGLS-LC100 and ESA-CCI, the highest classification accuracy classes were "forest", "tree cover areas," and "bare soil". Using a different approach based on a decision tree, Jung et al. (2020) found that Forest has the highest validation accuracy, although they obtained lower validation accuracy for rocky areas and desert habitat classes.

In contrast, wetlands and artificial habitats were more difficult to represent with land-cover maps. Wetland-related land-cover classes have the lowest classification accuracy in both land-cover maps. From a remote sensing perspective, wetlands are difficult to map because they are highly dynamic; rapid phenological changes occur throughout the year (Gallant 2015; Lumbierres et al. 2017). Remote sensing products at a global scale cannot distinguish small ponds or temporary water bodies (Pekel et al. 2016; Klein et al. 2017). Therefore, wetland land-cover classes had more omission errors, and this had a direct impact on the results of our model.

Artificial land-cover classes are also difficult to map because they tend to be more heterogeneous (Álvarez-Martínez et al. 2018), producing misclassifications among land-cover classes. It is difficult to separate some artificial land-cover classes from natural ecosystems (e.g., plantation from forest, grassland from cropland, lake from reservoir) with land-cover maps (Álvarez-Martínez et al. 2018). Overall, species richness and average abundance are often lower in artificial environments than in their natural equivalent, even if there is variation across different biogeographical contexts (Barlow et al. 2007; Newbold et al. 2015), and this introduces commission errors. Moreover, we found that artificial land covers are associated with some natural

habitat classes. This is likely a consequence of citizen science sampling bias produced by the greater accessibility of these habitats (Meyer et al. 2015). Because a high proportion of citizen science point location data are recorded in artificial land-cover classes, there is an increased probability that species primarily associated with natural habitats are reported there, so a data-driven method may associate some natural habitats with artificial land-cover classes. Addressing the biases in citizen science data is complex. For small datasets, accessibility maps are a useful tool for estimating sample bias (Monsarrat et al. 2019). However, at the global scale accessibility is driven by an interplay of geographic and socioeconomic factors that require complex modeling approaches in addition to more effective and structured data sampling techniques.

Land-cover maps have an associated error that varies among different land-cover classes (Grekousis et al. 2015) and continents (Buchhorn et al. 2020). Moreover, land cover classes that do not occur in extensive blocks have edge effects (Smith et al. 2002), which, combined with the mobility of animals, introduces errors in the association of the point data with the land cover. There are several differences between the two land-cover layers used to produce the translation tables that could determine the use of the table. The CGLS-LC100 has a resolution of 100 m, whereas ESA-CCI has a coarser resolution of 300 m, also CGLS-LC100 has an overall classification accuracy of 80.2% compared with 71.1% for ESA-CCI. Moreover, CGLS-LC100 avoids mosaic classes and in general; mapping areas with homogenous land cover is easier than mapping areas with heterogeneous land cover (Corbane et al. 2015; Álvarez-Martínez et al. 2018). The mosaic land-cover classes in the ESA-CCI table had very low odds ratio values and AUC. However, ESA-CCI has the advantage of being available for a longer time series (1992-2020 for ESA-CCI vs 2015-2019 for CGLS-LC100), which may be important for some applications. For both land-cover maps, we excluded some land-cover classes because of the lack of point localities. We recommend adding these land-cover classes manually when using the translation tables, according to the user's needs.

The coding of habitats to each species on the IUCN Red List could introduce some noise to the modeling process. Coding is based on the qualitative assessment by experts and is therefore susceptible to individual biases (Brooks et al. 2019; Santini et al. 2019). The current version of the IUCN Habitat Classification Scheme on IUCN's website is described as a draft version. We, therefore, recommend that IUCN update and improve this document and anticipate this would influence our odds ratio estimates. Our analysis also illustrates the complexity of linking habitat and land cover (Tomaselli et al. 2013). IUCN Habitat defines the environments of organisms (Kearney 2006), whereas land cover describes the biophysical material over the Earth surface (Grekousis et al. 2015). Different habitat or land-cover schemes, stemming from the particular

needs for each product, translate into different definitions of classes. This problem is exacerbated in transitional zones, where landscape heterogeneity is higher (Grekousis et al. 2015). While the FAO-LCCS scheme, scheme that defines the classes by both land cover maps, can better cope with the complexity of habitat description compared with other land-cover classifications schemes (Grekousis et al. 2015), it is important to understand that these classes are not optimized for biodiversity conservation studies (Joppa et al. 2016) so they do not directly relate to the habitat of species. Although the limitation in the point locality data, land cover and IUCN habitat, we consider that the translation models could be a useful tool for conservation.

Both the data-driven table and the expert-knowledge translation table (Santini et al. 2019) represented land-cover distribution inside the range better than random. However, our data-driven approach presents several advantages compared with an expert-knowledge approach. First, it defines the relationship between IUCN habitat and land-cover classes as a continuous variable, allowing greater flexibility in its application. For example, for producing AOH maps (Brooks et al. 2019), the user is able to decide a threshold of association to transform the results into a binary table according to the required balance between omission and commission errors. Second, a data-driven approach allows quantification of the uncertainty associated with the habitat to land-cover association. Third, it represents a more objective approach: several expert-knowledge translation tables exist, but there is no clear basis for choosing among them.

These data-driven translation tables have a direct applicability in the production of AOH maps (Brooks et al. 2019) because they provide a more objective way of removing unsuitable areas from the range map based on the information from the IUCN Habitat Classification Scheme and enable evaluation of uncertainties in the AOH maps. Our approach can be adapted to develop a translation table between any set of habitat codes for any set of species and any set of land-cover classes at a global or regional scale. As better data (including land-cover maps, species point localities, elevations, and habitat associations) become available, the translation table can be improved, ensuring objectivity and repeatability.

CHAPTER 3
AREA OF HABITAT MAPS FOR THE WORLD'S TERRESTRIAL BIRDS AND MAMMALS

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3.1 Abstract

Area of Habitat (AOH) is 'the habitat available to a species, that is, habitat within its range'. It complements a geographic range map for a species by showing potential occupancy and reducing commission errors. AOH maps are produced by subtracting areas considered unsuitable for the species from their range map, using information on each species' associations with habitat and elevation. We present AOH maps for 5,481 terrestrial mammal and 10,651 terrestrial bird species (including 1,816 migratory bird species for which we present separate maps for the resident, breeding and non-breeding areas). Our maps have a resolution of 100 m. On average, AOH covered 66±28% of the range maps for mammals and 64±27% for birds. The AOH maps were validated independently, following a novel two-step methodology: a modelling approach to identify outliers and a species-level approach based on point localities. We used AOH maps to produce global maps of the species richness of mammals, birds, globally threatened mammals and globally threatened birds.

3.2 Background & Summary

Knowing the distribution of species is crucial for effective conservation action. However, accurate and high-resolution spatial data are only available for a limited number of species (Rondinini et al. 2005; Rondinini & Boitani 2013). For mammals and birds, the most comprehensive and widely used global distribution dataset is the set of range maps compiled as part of the assessments for the International Union for Conservation of Nature (IUCN) Red List. These represent each species' distributional limits and tend to minimise omission errors (i.e. false absences) at the expense of commission errors (i.e. false presences) (Ficetola et al. 2014; Di Marco et al. 2017b). Therefore, they often contain sizeable areas that are not occupied by the species.

Maps of the Area of Habitat (AOH; previously known as Extent of Suitable Habitat, ESH) complement range maps by indicating potential occupancy within the range, thereby reducing commission errors (Brooks et al. 2019). AOH is defined as 'the habitat available to a species, that is, habitat within its range' (Brooks et al. 2019). These models are produced by subtracting areas unsuitable for the species within their range, using information on each species' associations with habitat and elevation (Beresford et al. 2011; Rondinini et al. 2011; Ficetola et al. 2015; Brooks et al. 2019). Comprehensive sets of AOH maps have been produced in the past for mammals (Rondinini et al. 2011) and amphibians(Ficetola et al. 2015), as well as subsets of birds (Beresford et al. 2011; Tracewski et al. 2016). The percentage of a species' range covered by the AOH varies depending on the methodology used to associate species to their habitats, and their habitats to land-cover, the coarseness of the range map, the region in which the species is distributed, and the species' habitat specialisation and elevation limits (Brooks et al. 2019). For example, Rondinini et al, 2011, found that, when considering elevation and land cover features for terrestrial mammals, the AOH comprised on average 55% of the range. Ficetola et al.(Ficetola et al. 2015) obtained a similar percentage when analysing amphibians (55% for forest species, 42% open habitat species and 61% for habitat generalists). Beresford et al. 2011, found that AOH covered a mean of 27.6% of the range maps of 157 threatened African bird species. In 2019, Brooks et al.(Brooks et al. 2019) proposed a formal definition and standardised methodology to produce AOH, limiting the inputs to habitat preferences, elevation limits, and geographical range.

AOH production requires knowledge on which habitats a species occurs in and their location within its range (Rondinini & Boitani 2013). Information on habitat preference is documented for each species assessed in the IUCN Red List (IUCN 2013), following the IUCN Habitats Classification Scheme (IUCN 2012b). However, IUCN does not define habitat classes in a spatially explicit way,

therefore, we used a recently published translation table that associates IUCN Habitat Classification Scheme classes with land cover classes (Lumbierres et al. 2021). Species' elevation limits were also extracted from the IUCN Red List.

We developed AOH maps for 5,481 terrestrial mammal and 10,651 terrestrial bird species. For 1,816 bird species defined by BirdLife International as migratory, we developed up to three AOH maps, one for the resident range, one for the breeding range and one for the non-breeding range. The maps are presented in a regular latitude/longitude grid with an approximate 100m resolution at the equator. On average, the AOH covers 66±28 % of the geographical range for mammals and 64±27 % for birds.

We used the resulting AOH maps to produce four global species richness layers: for mammals (Fig. 3.1), birds (Fig. 3.2), globally threatened mammals (Fig. 3.3) and globally threatened birds (Fig 3.4). The mammals and bird richness maps showed the already well-known patterns of species distribution with the hotspot in the tropic regions, however, their resolution allowed us to spot nuances produced by land destruction and other forms of habitat destruction, as seen in the Cerrato in South America or the Guinean lowland forest in Africa. The globally threatened mammal and bird richness maps showed that the highest number of threatened species was found in Southeast Asia.

The AOH maps have multiple conservation applications (Brooks et al. 2019; Hanson et al. 2020a; Strassburg et al. 2020), such as assessing species' distributions and extinction risk, improving the accuracy of conservation planning, monitoring habitat loss and fragmentation, and guiding conservation actions. AOH has been proposed as an additional spatial metric to be documented in the Red List (Brooks et al. 2019), and is used as an assessment parameter in the identification of Key Biodiversity Areas (IUCN 2016).

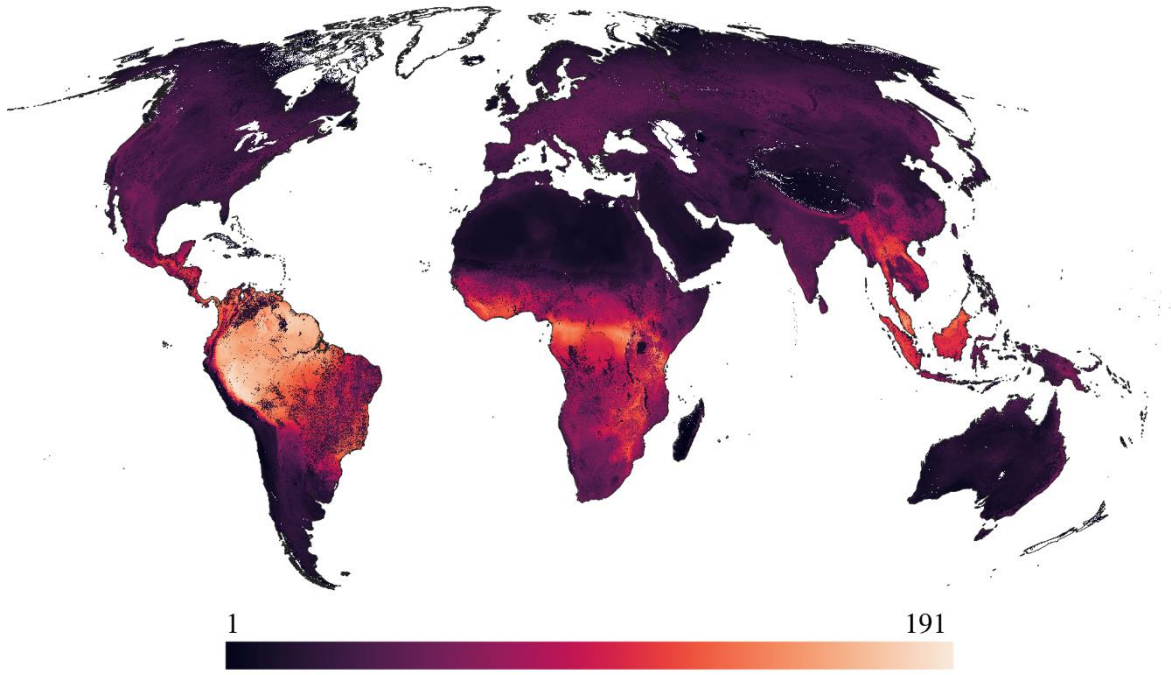

Figure3.1. Global terrestrial mammal richness at 100m resolution produced with the AOH map.

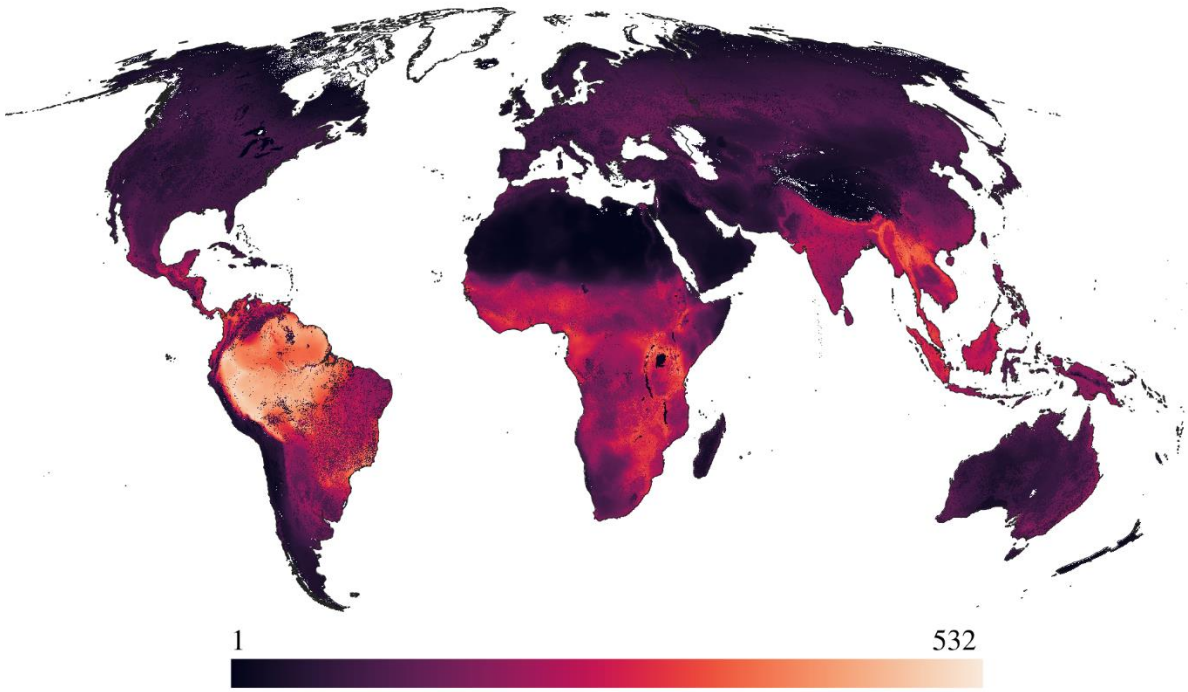

Figure 3.2. Global terrestrial bird richness at 100m resolution produced with the AOH map

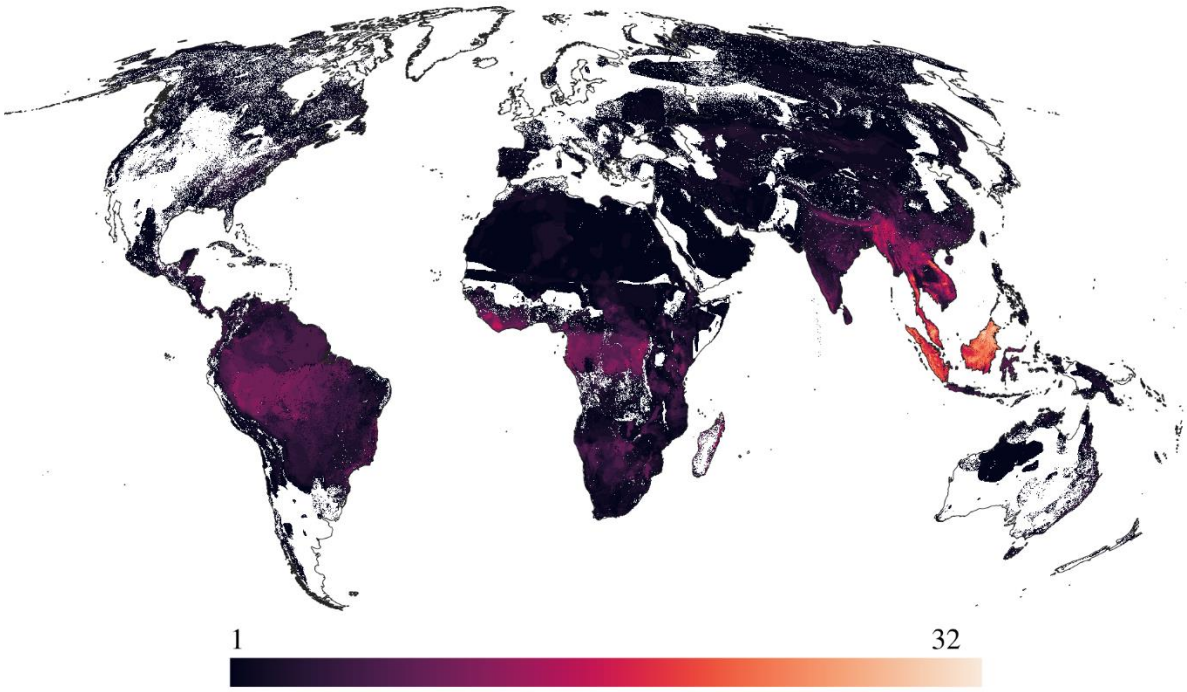

Figure 3.3. Globally threatened terrestrial mammal richness at 100m resolution produced with the AOH map

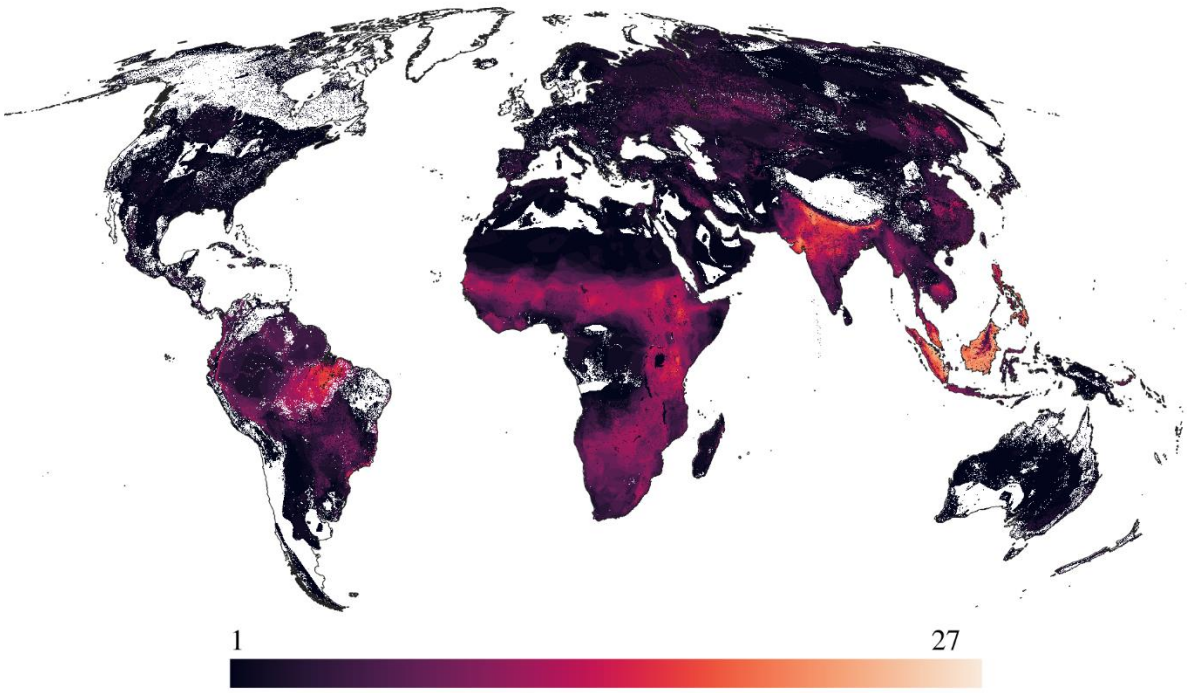

Figure 3.4. Globally threatened terrestrial bird richness at 100m resolution produced with the AOH map

3.3 Methods

We produced maps for species associated with at least one terrestrial habitat in the IUCN Habitat Classification Scheme (IUCN 2012b). We excluded a total of 342 species of mammals and 495 species of birds (6.2% and 4.6% out of 5,481 and 10,651 species, respectively). These comprised 135 mammals and 168 birds exclusively associated with marine habitats (i.e., marine neritic, marine oceanic, marine deep ocean floor, marine intertidal or marine coastal/supratidal), 29 mammals exclusively associated with caves and subterranean habitats, 131 mammals with no associated habitat codes, 8 mammals and 162 birds classified as Extinct, 1 mammal and 5 birds classified as Extinct in the wild, 12 mammal and 142 bird species that are restricted to small islands not included in the land-cover map we used, and 26 mammals and 18 birds that had null AOH, caused by errors in the coding of habitat and elevation (Dahal et al. 2021b).

Species may have more than one range polygon, coded according to presence (the species is or was in the area), origin (why and how the species is in the area) and seasonality (seasonal presence of the species in the area) (IUCN 2018). We used as a base for the AOH maps a predetermined subset of the IUCN Red List range (IUCN 2020) polygons for each species. Following the Global Standard for the Identification of Key Biodiversity Areas Guidelines (KBAs Standards and Appeals Committee 2019), we selected range polygons with *extant* and *probably extant* presence; *native*, *reintroduced*, and *assisted colonisation* origin; and *resident* seasonality for non-migratory species (all mammals and non-migratory birds; 8,979 species). For migratory birds (1,816 species), we kept separate the ranges for *breeding* (1,446 species), *non-breeding* (1,550 species) and a combination of *resident* and *uncertain* (1,290 species) seasonality. We provide an R script to merge the AOH sub-maps into a single composite map for each species. For 18 mammal and 22 bird species classified as Critical Endangered, there were no presence polygons coded as *extant* or *probably extant*. As the conservation of these species is a priority, we produced AOH maps using the *possibly extinct* polygon for these taxa.

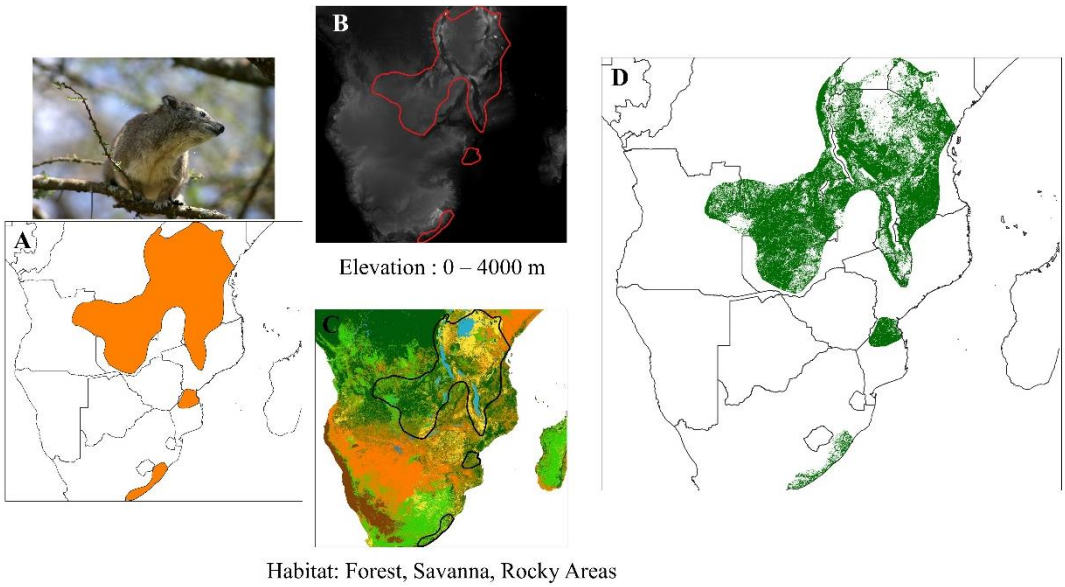

Figure 3.5. Example of the production of an AOH map for Dendrohyrax arboreus. Image A is the IUCN range map, image B a Digital Elevation Map, image C the habitat map derived from chapter 2 and image D the AOH of the species.

AOH maps are produced by subtracting unsuitable areas from range maps, using data on each species' associated habitat (Fig 3.5). As habitats in the IUCN Red List are not spatially explicit (although we note the existence of recently published maps (Jung et al. 2020)), we used a recently published translation table (Lumbierres et al. 2021) based on the Copernicus Global Land Service Land Cover (CGLS-LC100) (Buchhorn et al. 2019b, 2019a) and the European Space Agency Climate Change Initiative land cover 2015 (ESA-CCI)(European Space Agency, 2017). We developed the AOH maps based on CGLS-LC100 as CGLS-lC100 has a higher resolution and accuracy than ESA-CCI. CGLS-LC100 is in a regular latitude/longitude grid (EPSG:4326) with the ellipsoid WGS 1984 with a grid resolution of 1°/1008 or approximately 100 m at the equator, defining the resolution of the AOH maps. The translation table presented the relation between each habitat in the IUCN Classification Scheme and each land-cover class as a continuous variable. To create a binary table of association or non-association, Lumbierres et al. (2021) proposed three potential thresholds based on the tertiles of the positive association values of the table. We produced maps for the three proposed thresholds and evaluated the ratio of AOH area to range area. As the threshold increased, the ratio decreased, and the results were more similar to previous AOH maps (Rondinini et al. 2011). Dahal et al. (2021) evaluated these three thresholds and corroborated that an increase in the threshold did not reduce the performance of the AOH maps during validation. Therefore, we present the maps produced using the highest threshold (odds ratio> 1.7). Species' elevation limits were extracted from the IUCN Red List (IUCN 2020). To subtract the parts of the

range outside the elevation limits, we used the Shuttle Radar Topography Mission (USGS EROS Archive 2019) map, resampled at the resolution of the CGLS-LC100.

One of the main complexities of this analysis was the large amount of data generated in the process. Therefore, the AOH maps were produced using the GRASS GIS (GRASS Development Team 2020) software, which allows processing large amounts of raster data efficiently. The AOH production procedure consisted of four steps, following Rondinini et al. (2011): 1) Transforming the habitat codes of each species into land cover classes using the translation table (Lumbierres et al. 2021). 2) Creating a base map that combines the information on land cover and elevation 3) Creating reclassification files containing the information on land cover and elevation preferences for each species. 4) Reclassifying the base map based on the reclassification files to create the AOH for each species. We also created intermediate AOH maps clipped only by elevation or only by land cover, in order to explore the influence of each of these parameters on the final AOH. Once the AOH were produced, we calculated richness maps by stacking the AOH maps.

3.4 Data Records

The AOH data, including tables and maps, are stored in the Dryad Open Access Repository. The data are organised by taxonomic Class and Order with zipped folder by Order. In the case of birds, we separated migratory species from non-migratory species. In each class folder, maps are organised by taxonomic. AOH maps in GeoTiff. An additional folder contains the richness maps for each class of all species and of globally threatened species. In each folder, we include a table with information of the excluded species, indicating the reason for exclusion; and a table with the included species and the AOH/range ratio. For migratory birds, we included a table specifying which maps (breeding, non-breeding and resident) each species has and code to merge the different parts of the AOH.

3.5 Technical Validation

The accuracy of the AOH maps was assessed using a novel methodology developed by Dahal et al. and full details of the validation are provided there. This methodology allowed validation of AOH maps for species with or without point localities. Previous AOH maps were validated only using point localities and polygons of occurrence (Beresford et al. 2011; Rondinini et al. 2011; Ficetola et al. 2015), leaving some of the AOH maps unvalidated.

Our method employed a two-step approach. The first step identified potential systematic errors in the AOH maps using a modelling approach. This approach flagged 178 and 64 AOH maps for birds and mammals respectively that were carefully studied to identify the sources of potential errors. These potential errors were caused by inaccuracies in species' elevation limits, habitat coding or the translation table (Lumbierres et al. 2021) used to assign habitat to land cover. Work is currently underway to address these issues, and improved AOH maps will be available in the future for download at https://www.iucnredlist.org/resources/grid/spatial-data. A complete list of flagged maps can be found in Dahal et al, 2021.

The second step used point localities to validate the maps at the species level. To validate the AOH maps, the proportion of points localities falling inside the AOH (point prevalence) was compared with the A.O.H./range ratio (model prevalence). If point prevalence exceeded model prevalence, the AOH was assumed to be better than a random distribution within the species' range (Rondinini et al. 2011). This was done for the 4,889 birds (46% of all bird species) and 420 mammals (8% of all mammal species) that had available point locality data (Dahal et al, 2021). For mammals, this represented 157 species more than in a previous set of AOH (Rondinini et al. 2011) maps published in 2011. AOH maps were better than random for 95.9% bird and 95 % mammal species. The unavailability of point locality data for half of bird species and most mammal species remains a major limitation of the validation analysis. However, the first step of the method allowed us to assess at least the general soundness of AOH maps for species that did not have suitable point localities for validation.

3.6 Usage Notes

The maps are presented in raster byte GeoTIFF format. The values of the maps are 1 for the AOH area and Null for the background. The geographical extent of each map is defined by the species' range. Each species map is presented separately with the species binomial name, and the genus and specific epithet separated by an underscore. For migratory birds we produced three different maps, that are coded using, R, B and N for resident, breeding and non-breeding AOH maps, respectively. We present code written in R to merge the different AOH maps for migratory species according to the needs of the user. For species with null AOH we recommend using the mapped range.

3.7 Code Availability

The code to produce the AOH is derived from code produced by Rondinini et al. (2011). AOH maps are produced reclassifying a base map that contains information on elevation and land cover. The geographical range maps are used to mask the areas outside the distribution of the species. Each species has a reclassification file that indicates which land cover classes and elevations are suitable. To transform the habitat information into land cover we used the translation table (Lumbierres et al. 2021). The code is both in GRASS and R.

3.7.1 Base map

The base map is the map that is reclassified to produce the AOH. Each cell value is a combination of land cover and elevation, where the three first digits represent land cover and the three last digits elevation in m/10.

```
# GRASS SCRIPT
# Grass location and mapset
grass -c -e EPSG:4326 /data/grassdata/latlong
grass -c -e /data/grassdata/latlong/AOH
# Import data
r.import in=land_cover out=land_cover # Import data
r.import in=srtm out=srtm
# Base map calculation
r.mapcalc expression="base_map=(land_cover*1000)+(round(srtm/10))"
```

3.7.2 Reclassification Files

The GRASS reclass function has a specific format for the reclassification instructions. The script produces reclass files to apply to the base map in GRASS to produce maps of area of habitat for terrestrial species. It reads a file that contains land cover associations, with the following column headers: species name, one column per land cover class (with numeric column names for land cover; e.g., 10, 20, 210), and two columns representing elevation range (elevation_min and elevation_max). If the elevation range for a species is unrecorded, it is set to 0-9000 m.

```
# R SCRIPT
setwd()
options(scipen=99999)#Disable scientic notation
```

```
lc <- function(x){
  as.numeric(substr(x, 2, nchar(x)))*1000
}
sp_lc_el <- fread("sp_land_cover_elevation_file")
sp_lc_el$elevation_min<-round(sp_lc_el$elevation_min/10,0) # min
sp_lc_el$elevation_max<-round(sp_lc_el$elevation_max/10,0) #max
ncol <- ncol(sp_lc_el)
setwd("reclass_files_folder") # Path where to safe reclassification
files
for(i in 1:dim(sp_lc_el)[1]){
  for(j in 2:(ncol-2)){
    if(sp_lc_el[i,j]==1){
      if(sp_lc_el[i,(ncol-1)]==0 & sp_lc_el[i,ncol]==900){
        write.table(paste0(lc(names(sp_lc_el)[j]),
                           " thru ",lc(names(sp_lc_el)[j])+900," =
1"),
       file=paste0(sp_lc_el[i,1]),
append=T,quote=F,row.names=F,col.names=F)
      }
      if(sp_lc_el[i,(ncol-1)]==0 & sp_lc_el[i,ncol]<900){
        write.table(paste0(lc(names(sp_lc_el)[j]),," thru ",

lc(names(sp_lc_el)[j])+sp_lc_el[i,ncol]," = 1"),
      file=paste0(sp_lc_el[i,1]),
append=T,quote=F,row.names=F,col.names=F)
      }
      if(sp_lc_el[i,(ncol-1)]>0 & sp_lc_el[i,ncol]==900){

write.table(paste0(lc(names(sp_lc_el)[j])+sp_lc_el[i,(ncol-1)],
                           " thru ",lc(names(sp_lc_el)[j])+900, " =
1"),
      file=paste0(sp_lc_el[i,1]),
append=T,quote=F,row.names=F,col.names=F)
      }
      if(sp_lc_el[i,(ncol-1)]>0 & sp_lc_el[i,ncol]<900){

write.table(paste0(lc(names(sp_lc_el)[j])+sp_lc_el[i,(ncol-1)],
```

```
                              " thru ",

lc(names(sp_lc_el)[j])+sp_lc_el[i,ncol]," = 1"),
     file=paste0(sp_lc_el[i,1]),
append=T,quote=F,row.names=F,col.names=F)
      }
    }
  }
  write.table("* = 0",file=paste0(sp_lc_el[i,1])
                                  ,append=T,quote=F,row.names=F,col
.names=F)
  write.table("end",file=paste0(sp_lc_el[i,1])
                                  ,append=T,quote=F,row.names=F,col
.names=F)
}
```

3.7.3 AOH production

AOH is confined inside the geographical range. The geographical range maps can be downloaded from https://www.iucnredlist.org for mammals, and http://datazone.birdlife.org/species/requestdis for birds. The ranges are imported into GRASS and rasterised. The ranges are used to mask the area outside the species distribution. Inside the non-masked areas, the base map is reclassified using the reclassification file.

```
# GRASS SCRIPT
for i in `cat species_list’ `
do
v.in.ogr input=$i.shp output=vec_$i snap=1e-09 --overwrite
g.region -a vector=vec_$i res=0:00:03.571429
v.to.rast  input=vec_$i  type=area  use=val=1  output=ras_$i  --
overwrite
r.mask raster=ras_$i --overwrite
r.reclass in=bm_CGLS@base_maps out=$i rules=$i --overwrite
r.mapcalc "$i = $i" --overwrite
r.mask -r
done
```

CHAPTER 4
EVALUATING THE USE OF IRREPLACEABILITY TO IDENTIFY KEY BIODIVERSITY AREAS, AND THE EFFECTS OF GEOGRAPHICAL SCALE

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4.1 Abstract

Sites qualify as Key Biodiversity Areas (KBAs) under KBAs Criterion E if they have a very high irreplaceability value (>0.9 on a 0-1 scale) derived from a quantitative spatial prioritisation analysis. However, the application of this Criterion is still in its infancy as it was only recently introduced in the KBAs context. Irreplaceability is a measure of how important a specific area is for efficiently achieving conservation objectives. The irreplaceability of a site is determined by both the biodiversity found within it and the biodiversity contained in the other sites considered in the analysis, meaning it will be affected by the geographical scale of the analysis and the set of biodiversity features analysed. For country-level analyses (which are likely to be the norm for

KBAs identification), it is important to consider whether all species should be included or only those restricted to the country. We explored the identification of KBAs based on Criterion E for eight countries in two geographical regions, South America and East Africa, for terrestrial mammals. We repeated analyses at a regional level (including all species in the region), and at a country level performing separate analyses for each country. In the South American analysis, we found that, on average, 47% of regionally irreplaceable planning units were not represented in country-level analyses, while country-level analyses mainly represented a subset of the regional ones. The planning units selected as irreplaceable exclusively at the regional level held more species than the other planning units considered in the analysis, while the planning units selected at the country level had species with a smaller AOH extent, on average. These results indicated that at the regional level, irreplaceability is driven by endemic species and species richness, while at the country level, exclusively by endemic species. In fact, for the country-level analysis, we found that the number of irreplaceable planning units in a country generally was only marginally affected by criteria for species inclusion in the analysis (all species vs country-restricted). For some African counties, the analysis produced very few or no highly-irreplaceable planning units, but patterns of highly-irreplaceable planning units appeared when we increased the targets (i.e. the proportion of each species' range to be included). This could indicate that the current targets were too low for these countries. We conclude that the results obtained from the current formulation of Criterion E are affected by the geographical scale and region in which it is applied. The KBAs Standards and Appeals Committee can take some actions to make the analysis more robust, such setting the scale of application at the regional level and revising the targets However, for this last one more testing is required, including evaluating the use of proportional versus absolute targets, and the effect in different geographical regions and taxa.

4.2 Introduction

Key Biodiversity Areas (KBAs) are sites contributing significantly to the global persistence of biodiversity (IUCN 2016) and are an essential conservation tool. The KBAs identification process is a bottom-up process led by the relevant national stakeholders. KBAs are delineated to be potential management units. KBAs are used to guide and measure the effectiveness of site-based conservation, such as protected areas and other effective area-based conservation measures (OECMs) (Donald et al. 2019a). KBAs form the most comprehensive set of sites of importance for biodiversity (Visconti et al. 2019), and coverage of KBAs by protected areas and OECMs has been proposed as an indicator for monitoring progress towards Target 3 of the post 2020 Global

Biodiversity Framework (CBD 2021), building on its existing use as an indicator for Sustainable Development Goals 14 and 15 (United Nations 2021).

KBAs are identified according to a set of criteria with quantitative thresholds, which are outlined in the *Global Standard for the Identification of Key Biodiversity Areas* (KBAs Standard) (IUCN 2016). Criterion E is based on irreplaceability, a metric derived from systematic conservation planning. Systematic conservation planning is a structured, systematic approach to identifying conservation areas important for biodiversity and prioritising and implementing conservation actions (Margules & Pressey 2000). Irreplaceability is defined as either (a) the likelihood that an area will be required as part of a set of areas that achieve particular biodiversity targets (Ferrier et al. 2000) or (b) the extent to which the options for achieving the targets are reduced if the area is unavailable for conservation (Pressey et al. 1994). Sites qualify as KBAs under Criterion E if they have a very high irreplaceability value (>0.9 on a 0-1 scale) derived from a quantitative spatial prioritisation analysis (IUCN 2016). Criterion E follows a complementarity-based approach to measure how important a specific area is for the efficient achievement of conservation objectives. Its incorporation into the KBAs framework attempts to reconcile threshold-based approaches and the systematic conservation planning approach (Di Marco et al. 2016; Smith et al. 2019).

Irreplaceability as a focus for a Criterion to identify KBAs poses some challenges, as it has not been previously applied in this context. The analytical parameters necessary for Criterion E - such as irreplaceability threshold, targets, and the scale of application - require testing to verify that the Criterion is in line with the overall KBAs methodology and is robust in terms of spatial prioritisation. Especially attention is necessary to study the effects of the planning unit size and number of taxonomic groups and the geographical scale on the irreplaceability scores. Moreover, to study surrogacy among Criterion E and the other KBAs criteria.

As the irreplaceability of a site depends on both the biodiversity found within it and the biodiversity contained in the other sites considered in the analysis, it will be affected by the geographical scale of the analysis and the set of biodiversity features (e.g. species) analysed. As KBAs are globally significant sites for biodiversity, the contributions of a site for a given biodiversity element should be measured in relation to the global population (for species) or extent (for ecosystems) (IUCN 2016). This presents some challenges, as calculating irreplaceability at a global scale (and at an appropriate resolution for application to sites) requires considerable computing power, and global species distribution data may be less accurate than national data for well-studied countries. Moreover, the KBAs Standard specifies that the identification of KBAs must be led at the country

level. Therefore, it is necessary to establish mechanisms to calculate irreplaceability at the country level that reflect global importance for biodiversity.

The KBAs Standards specified that irreplaceability analyses must be conducted at a global scale or focus only on the endemics from the region analysed or set the targets to reflect the fraction of the global population size of each species that is included in the study area. However, these three options could result in different irreplaceable planning units' selection. In a country-level complementarity analysis of species data, it is important to consider which species should be included, as species' distributional limits do not typically match country borders. The two extremes would be to include all species occurring in that country, even those whose distribution only marginally overlaps the country, or include only endemic species (those occurring only in that country). Both cases can result in suboptimal solutions. Including all the species can cause an edge effect, whereby planning units on the border are preferentially selected, even if they are not irreplaceable at a global scale. In contrast, including only endemic species can cause irreplaceable planning units for non-endemic species to be omitted.

Once the geographical scale is set, three parameters largely determine which planning units are considered highly irreplaceable: the conservation targets, the irreplaceability threshold, and the spatial resolution of analyses (i.e. grid size). For KBAs Criterion E, these parameters are specified in the KBAs Standard. The conservation targets identify the contributions of each conservation feature to the system, and in systematic conservation planning, they are used to define the conservation goals of the analysis. The irreplaceability threshold is an arbitrary value set at 0.9 (on a 0 to 1 scale) in Criterion E and indicates which planning units are considered significant for the global persistence of biodiversity. The spatial resolution of the analysis influences irreplaceability because larger grid cells (i.e. planning units) have higher biodiversity content and higher irreplaceability. This value has been set to between 100 km^2 and 1,000 km^2 in the KBAs Standard, to standardise its application.

Here, we explored the identification of KBAs based on Criterion E for two geographical regions, South America and East Africa. In each region, we tested the Criterion at different spatial scales. At the country level, we tested how irreplaceability changes depending on the number of species included in the analysis and their endemism level. We then tested how the irreplaceability values differ when modifying the conservation targets and the irreplaceability thresholds. Based on our results, we make recommendations for the appropriate application of Criterion E, in order to inform the KBAs Guidelines (KBAs Standards and Appeals Committee 2020).

4.3 Methods

Our analyses focused on four countries in South America (Colombia, Ecuador, Peru, and Venezuela) and four countries in East Africa (Kenya, Uganda, South Sudan and Ethiopia). The two regions have moderate to high biodiversity richness and endemism (Table 4.1) and represent and are area that with a very big KBAs network. For the purposes of our analyses, we ignore the shared biodiversity with adjacent countries; this allows evaluating clearly the effect of rescaling the targets between the global and regional analysis. The biodiversity data used were Area of Habitat (AOH) maps for the world terrestrial mammals (Lumbierres et al. n.d.; Dahal et al. 2021a), at a resolution of approximately 100 m WGS84. We used AOH instead of geographical range maps (Hanson et al. 2020a) because AOH reduces the commission errors of range maps and allows an accurate identification of the irreplaceable areas (Bombi et al. 2011). The parameters of the analysis followed the ones established in the KBAs Standard (IUCN, 2016) and the KBAs Guidelines (KBAs Standards and Appeals Committee 2020). The planning units (i.e. the spatial units in which the study area was subdivided), were Mollweide projection equal area grids of 100 km^2. The mammal distribution data was reprojected, and we calculated the area of each species' AOH inside each planning unit. The cost of the planning units is not considered in the KBAs Standard because KBAs represent sites of importance for biodiversity but not necessarily sites requiring conservation action, hence we only considered the actual land area of each planning unit as a "cost surface" assigning a value of 1 to inland planning units and scaled fractional values to coastal ones, corresponding to the proportion of land area vs ocean area. The planning units with a cost smaller than 0.20 were discarded as most of their surface was cover by water.

Table 4.1*: Characteristics of each of the study regions and the mammal species included in the analysis*

	South America	**East Africa**
Number of species	755	393
Number of planning units	37,754	27,031
Mean % endemic species by country	46%	38%
Mean AOH extent (km^2)	217,421	156,486

The KBAs Standard defines the targets to be used in the application of Criterion E in terms of number of individuals or distribution. As we used AOH data, we used the distribution targets. The

Standard states that the largest of the following options should be selected as the target for each biodiversity feature: (i) 1,000 km^2 of the range, (ii) the total area where the species occurs if the species' AOH is smaller than 1,000 km^2, (iii) the area necessary to include 1,000 mature individuals, or (iv) the area necessary to ensure the global persistence of the species as measured by quantitative viability analysis. I did not include the fourth option because this information is available for a very limited number of species at a global scale.

To determine whether individual planning units met the third of these options, it was necessary to have information on population density for each species. However, such data are not available for all species (Santini et al. 2018). Therefore we modelled density as a function of body mass and trophic level, as these data are more widely available for mammals (Soria et al. 2021). We modelled the relationship between these variables as a log-log function, with taxonomic order as a random effect in a mixed-effect model (Silva et al. 2000) (Appendix S4.1). The total number of species with a density higher than one individual per km^2 was 26 for South American and 51 for East Africa.

Calculating irreplaceability is computationally intensive, so different tools have been developed to approximate irreplaceability (Moilanen et al. 2009). In this analysis, we used Marxan, which is built on simulated annealing to solve the spatial prioritisation problem in an efficient way, and selection frequency to approximate irreplaceability. Selection frequency is the proportion of times a planning unit is selected within a spatial solution, out of all the identified solution that meet all targets (Ball et al. 2009). To calculate Selection Frequency we performed 1000 Marxan runs for each analysis with 1 million iterations each and set a penalty factor of 100, this value is set to prioritise meeting the conservation targets instead the cost (Di Marco et al. 2016; Serra-Sogas et al. 2020).

For each study region we ran both a "regional-level analysis", combining all four countries in the region, and "country-level analyses", separate for each country (Fig. 4.1). To evaluate the effect of including species only marginally occurring in a country, we repeated country-level analyses using incremental thresholds of AOH overlap for species inclusion in the country (>0%, >5%, >10%, >15%, >20%, >25%, >30%, >40%, >50%, >75%, >99%). To evaluate the differences in the number and distribution of irreplaceable planning units, we counted the number of highly irreplaceable (>0.9) planning units in the regional-level and country-level analyses. We then compared the planning units that were selected in each analysis.

To understand the reasons for the different number of planning units selected in the region- and country-level analyses, we identified three sets of planning units: those selected only in the regional-level analysis, those selected in both regional- and country-level analysis, and those not selected in either analysis. We did not include the planning units only selected in the country-level analysis as the number was marginal. We did not compare the planning units in East African countries, as for most of the counties, there were no irreplaceable planning units. We calculated the number of species per planning unit and the mean AOH extent per species in each planning unit for each set of planning units. We then compared the results of each set and tested its significance with an ANOVA test and Tukey multiple pairwise comparisons. We also compared different metrics between the South American and the East African regions. We calculated the percentage of overlap between the country and the AOH, the mean AOH extent, and the ratio between targets and the AOH extent for each country. We also tested the significance with an ANOVA and compared the two regions' results with Tukey multiple pairwise comparisons.

To test the effects of the irreplaceability threshold, we used the previous analysis and counted the number of planning units with irreplaceability values higher than 0.7, 0.5, 0.3. To evaluate the effects of the targets, we repeated the analysis with targets multiplied by 2, 5, and 10. We did not test the reduction of targets because reducing the targets produces no irreplaceable planning units.

4.4 Results

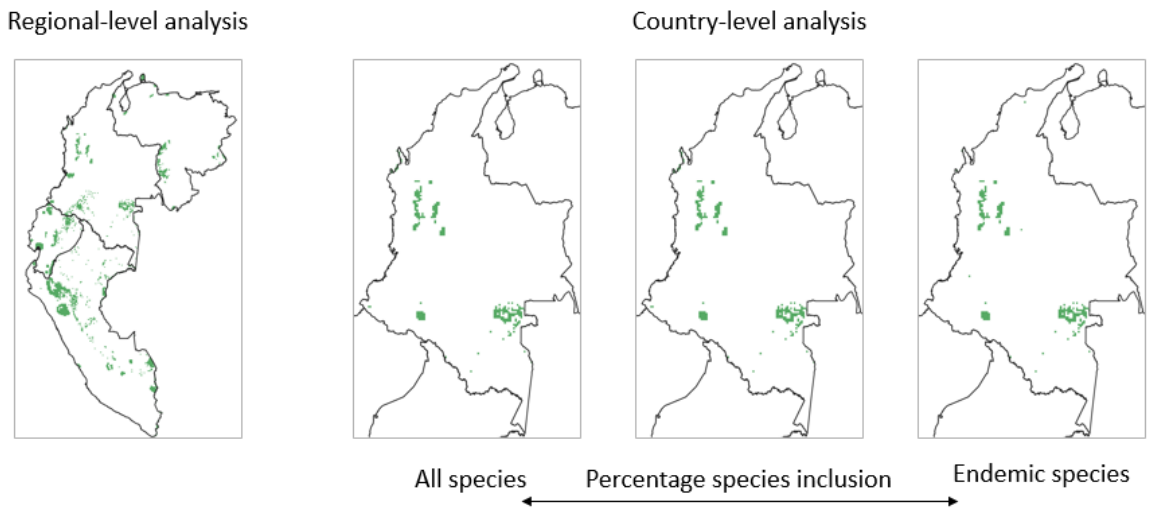

Figure 4.1. Example of maps showing calculated irreplaceability for mammals in 100-km^2 planning units in Colombia.

We calculated and mapped the irreplaceability for the regional-level analysis and then for the country-level analysis with species with different percentages of their AOH included (Fig. 4.1). We counted the number of planning units with irreplaceability higher than 0.9 separately for the South America analysis and the East Africa analysis (Fig 4.2).

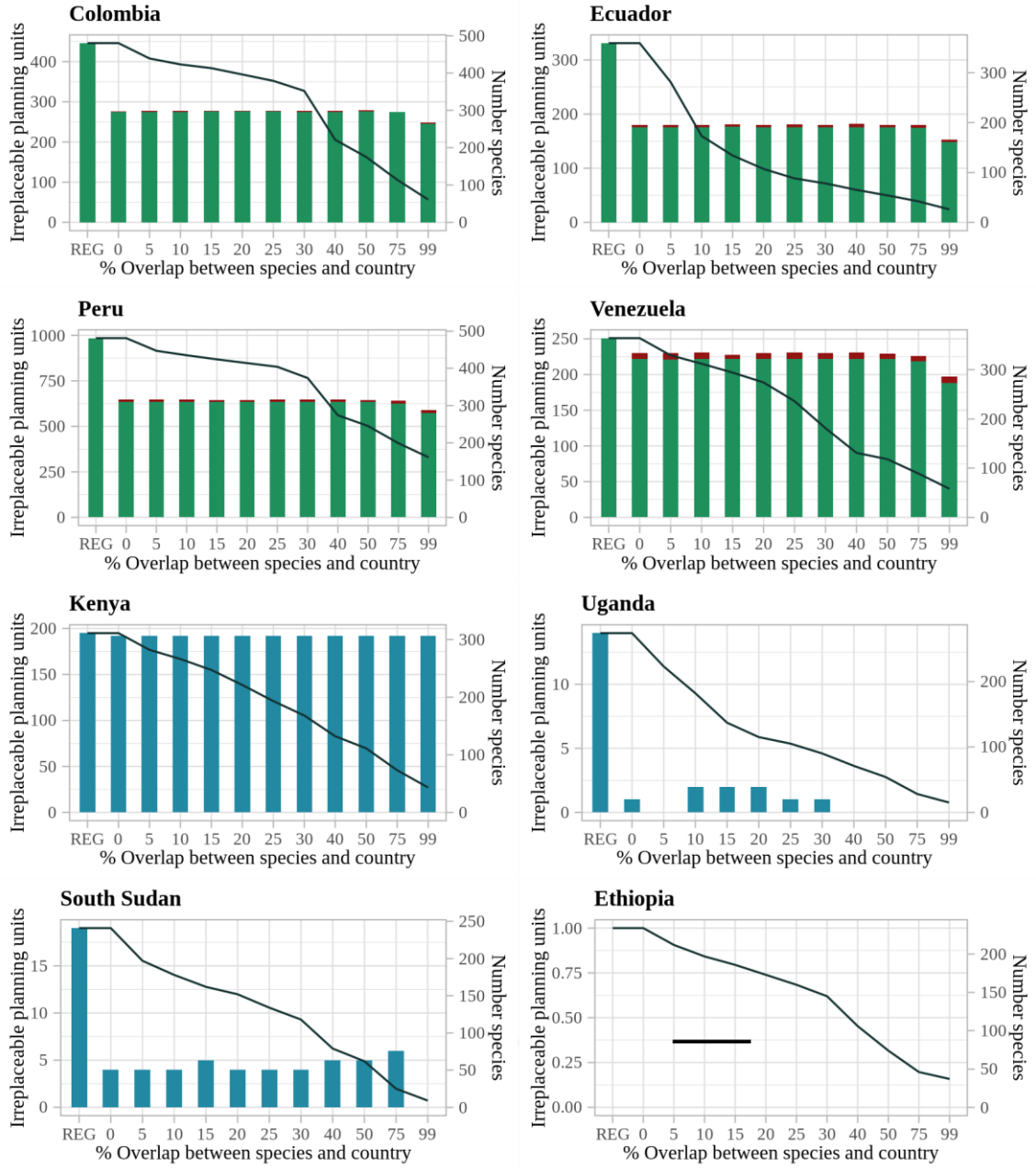

Figure 4.2. Number of planning units with irreplaceability higher than 0.9, calculated using Marxan selection frequency, in each country. The first column of each graph represents the number of planning units selected at regional-level analysis for the country and the rest of the columns the planning units selected country-level analysis with incremental thresholds of range overlap for

species inclusion in the country. The black line represents the number of species included at each at each Marxan run.

We found more irreplaceable planning units in the regional-level analysis than in the country-level analysis for most countries, with the latter largely representing a subset of the former, particularly for Colombia, Ecuador, Peru, Uganda and South Sudan. The number of irreplaceable planning units generally did not differ with the threshold used for including species in the country-level analysis, even though the number of species decreased rapidly with higher thresholds for the proportion of the species' AOH occurring in the country. An exception was when the threshold was set at >99% (i.e. including only nationally endemic species), where we found a slight reduction in the number of planning units identified. This pattern was most evident in South America and Kenya. In Uganda and South Sudan, there was no clear pattern when comparing the number of planning units selected with different thresholds of species inclusion. In Ethiopia, there were no highly irreplaceable planning units.

To explore the characteristics of sites selected under regional and/or country analyses, we calculated the number of species (Fig. 4.3) and the mean AOH extent per planning unit (Fig. 4.4). We characterised the planning units in three groups: those selected only in the regional-level analysis, those selected in both regional- and country-level analysis, and those not selected in either analysis. For Colombia, Ecuador and Peru, the number of species per planning unit was highest in the regional analysis (Tukey test $P < 0.05$; Appendix S4.2), while mean AOH extent was lowest in the country-level analysis. These also were the countries with the most significant differences between the regional- and country-level analyses. In Venezuela, we found the opposite pattern for the number of species and the AOH extent. This country had the lowest differences between the regional- and country-level analyses.

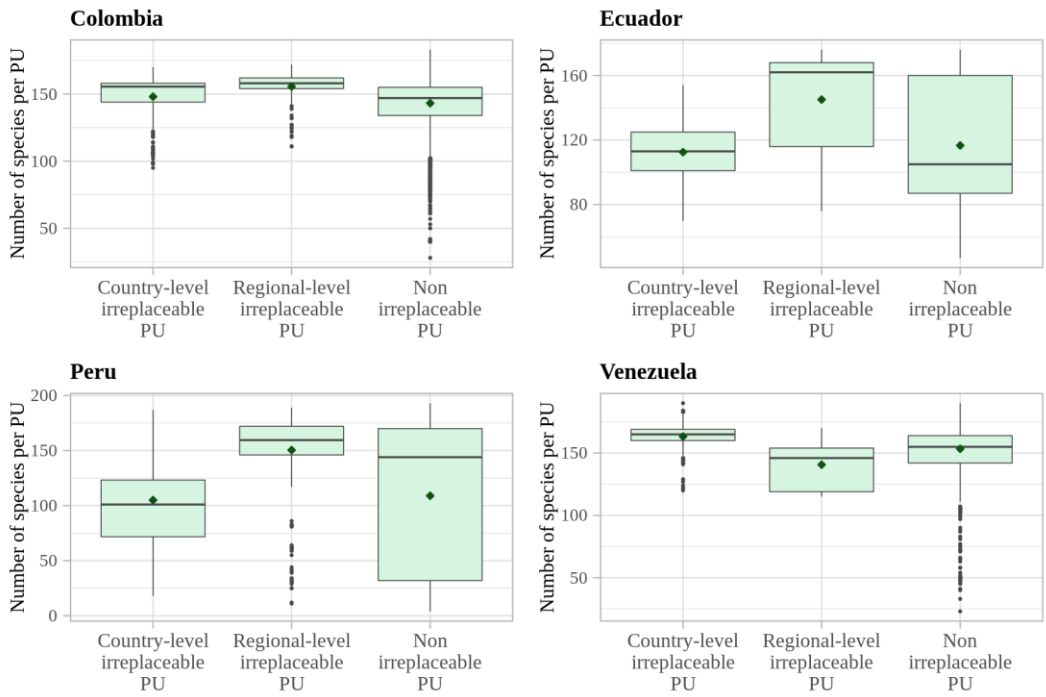

Figure 4.3. Boxplots of the number of species per planning units in three groups of planning units: those selected only in the regional-level analysis, those selected in both regional and country-level analysis, and those not selected in either analysis. Green dot is the mean values for each group.

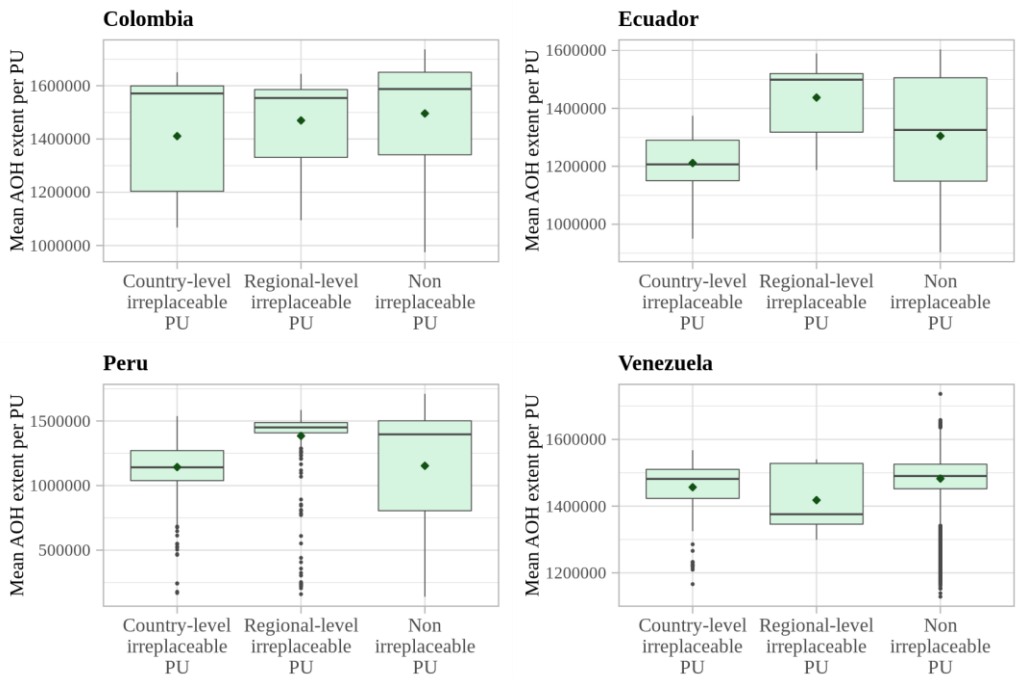

Figure 4.4. Comparison of the mean Area of Habitat extent per planning units in three groups of planning units: the those selected only in the regional-level analysis, those selected in both regional and country-level analysis, and those not selected in either analysis. Green dot is the mean values for each group.

We calculated different metrics to compare the two study regions (Fig 4.5, Appendix S4.3). The first metric was the percentage of overlap between species and countries. The mean was similar among the countries for the two regions, but in South America, the number of species that overlap entirely with a country was higher than in East Africa, indicating a higher number of endemic species. The second metric was the mean AOH extent per country. In South American countries, the mean AOH extent were bigger that in East African (ANOVA $p < 0.05$; Appendix S4.2), but also de standard deviation was the biggest. The third metric was the ratio between the target and AOH extent. This metric indicates the proportion of the AOH considered in the target (e.g. a value of 1 means that all the AOH is a conservation target). For both study regions, this value was very small. However, the mean value was higher for South American countries than East Africa (ANOVA $p < 0.05$; Appendix S4.2). Moreover, in South American counties and Uganda, there were several species that the target considers their entire AOH.

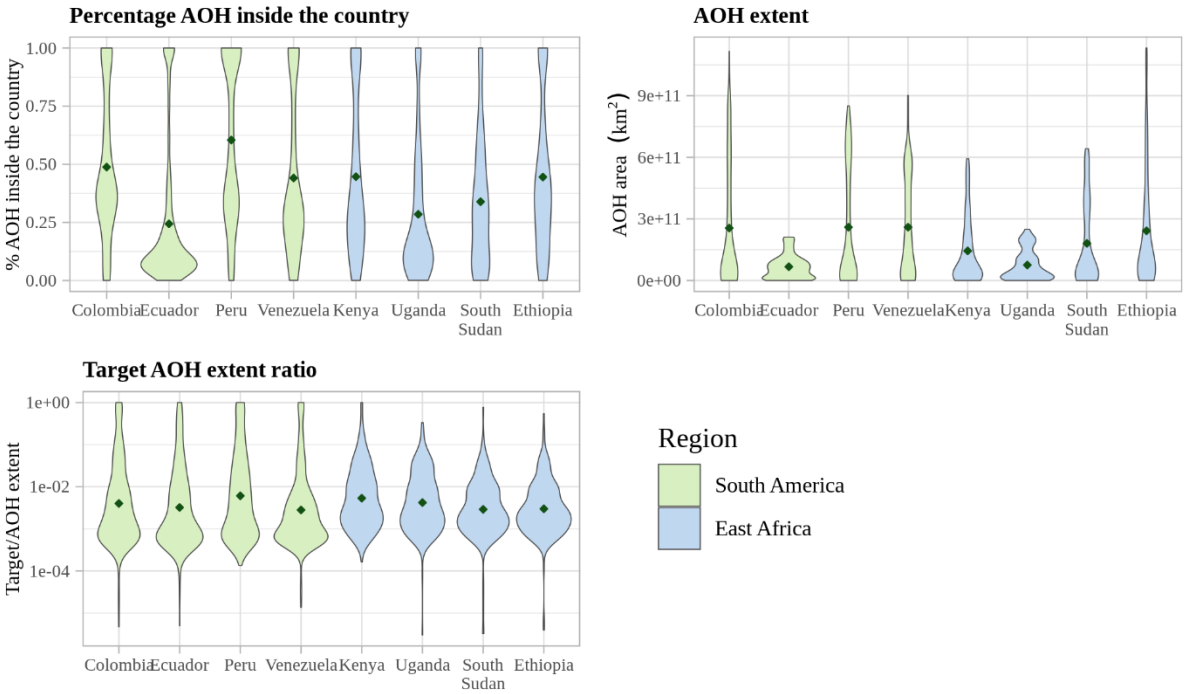

Figure 4.5. Comparison of the percentage of AOH inside the country, AOH extent and Target AOH extent ratio among the countries of analysis. Green dot is the mean values for each country.

Figure 4.6. Number of planning units with irreplaceability higher than 0.9, 0.7, 0.5 and 0.3 calculated using Marxan selection frequency, in each country. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds.

Decreasing the irreplaceability threshold to 0.7, 0.5 and 0.3 increased the number of planning units selected in all cases (Fig. 4.6). However, there were differences between countries and the regional

and the country-level analysis. For South America regional analysis, with a 0.7 irreplaceability threshold, the was a 7% increase in the number of planning units, and with a 0.3 threshold, a 56% increase. For the country-level analysis, the same thresholds increased the number of planning units by 14% and 91%, respectively. Consequently, decreasing the irreplaceability threshold reduced the magnitude of the difference between the number of planning units selected in the regional vs country-level analyses. For Uganda and South Sudan region analysis, only the 0.3 irreplaceability threshold increased the number of planning units. For the country-level analyses, the 0.7 irreplaceability threshold increased 14% the number of planning units, and the 0.3 threshold increased the number of planning units considerably by more than1000%, except for endemic species. In Ethiopia, more planning units were selected with lower irreplaceability thresholds, but no clear pattern was found.

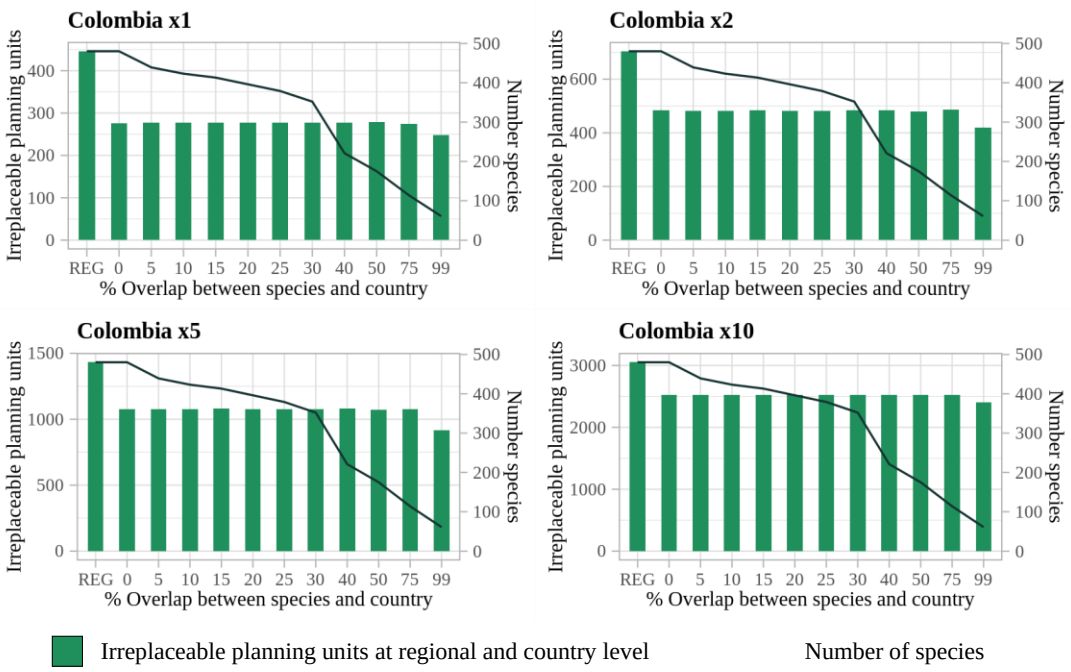

Figure 4.7. Number of planning units in Colombia with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds.

The results of multiplying the targets by 2, 5, and 10 showed an increase in the number of irreplaceable planning units in all the cases, although we still found a higher number of irreplaceable planning units in the regional-level than in the country-level analysis. However, in South America (Fig. 4.7 and Appendix S4.4), increasing the targets reduces the difference between the number of planning units selected in the regional vs country-level analyses. In the case of Ethiopia, South Sudan, and Uganda (Fig. 4.8 Appendix S4.5), increasing the targets resulted in a

similar pattern to those we observed in South America. In the case of Ethiopia, it is clear that with the increase in the targets, some irreplaceable planning units were selected. This indicated that targets for mammals might be too small to detect any planning units in this case.

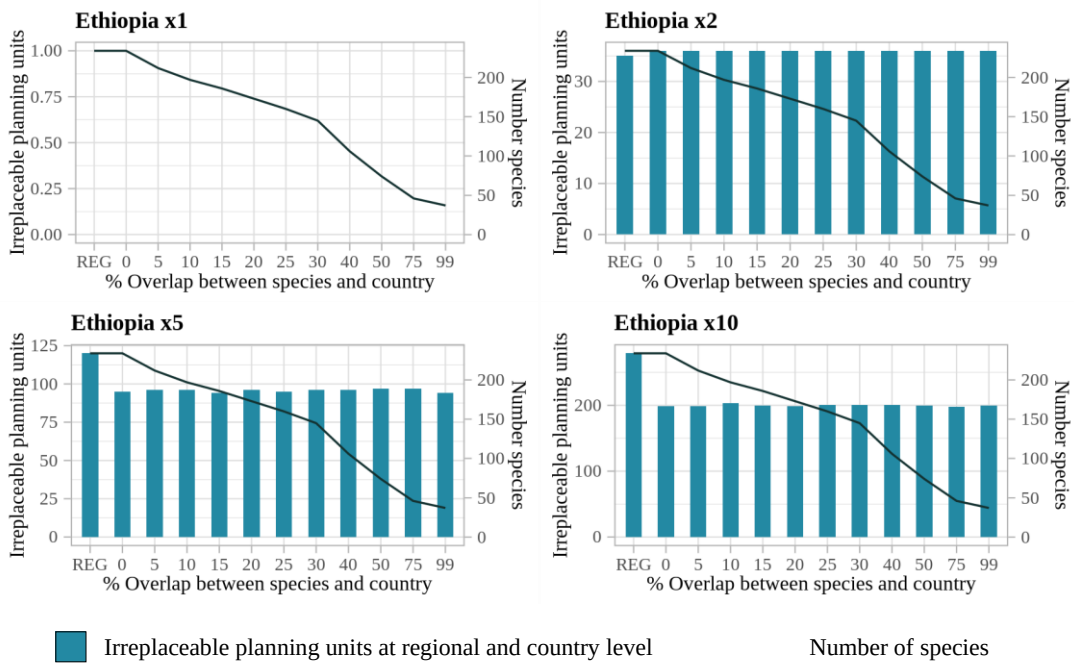

Figure 4.8. Number of planning units in Ethiopia with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds.

4.5 Discussion

We tested the effect of the geographical scale on the irreplaceability calculation following the definition of Criterion E in the KBAs Standard. The results showed that for most countries, there were more irreplaceable planning units in the regional-level analysis than in the country-level analysis, with the latter mainly representing a subset of the former. At the same time, we explored criteria for species inclusion according to their range overlap with the country and found that the number of irreplaceable planning units selected generally did not differ, except when only endemic species were included.

The planning units selected exclusively at the regional level were characterised by a larger number of species, which on average had larger AOH extents, compared with planning units that were also selected at the country level. This indicated that the irreplaceability of these planning units was

driven by their species richness rather than the presence of country-restricted species. Moreover, this demonstrates that the scale at which Criterion E was applied influenced the number and distribution of irreplaceable planning units.

The results at the country level indicated that irreplaceability was driven mainly by endemic species. Planning units selected at the country level contained species with the smallest AOH extent, indicating that irreplaceability is driven by both endemic and restricted-range species. Therefore, with the current formulation of Criterion E, the percentage of species inclusion into country-level analysis seems to have little influence on the result, at least for mammal species, which (as with birds) have, on average, large ranges.

Previous studies have already linked irreplaceability with richness and aggregation (Gardner et al. 2015) and endemism and restricted-range species (Ferrier et al. 2000; Di Marco et al. 2016). However, our results suggest that with the current absolute targets of KBAs Criterion E, the relationship between richness and irreplaceability is linked to the geographical scale of the analysis. The difference between the number of planning units selected at the regional and country-level remained even when increasing the targets, although the gap was reduced. The addition of new taxa could increase this effect even more.

For some African counties (Uganda, South Sudan, and Ethiopia), the analysis produced very few or no highly irreplaceable planning units. Each of the runs for species inclusion returned seemingly random results with different numbers and distribution of the planning units, and when reducing the irreplaceability threshold to 0.5 or lower, the number of selected planning units increased considerably. In each run, Marxan selected a different solution, because multiple solutions had similar costs, therefore, no planning units were highly irreplaceable (Kark et al. 2009). When we increased the targets, patterns of highly irreplaceable planning units started to appear. African countries had fewer endemic species than South American countries, and although the average AOH extents were similar, the target-to-AOH ratios were smaller. The African result could indicate that the current targets are too low for most species (those that are not range-restricted) to make a real difference in the definition of the irreplaceability locations. However, we investigated only two regions and one taxonomic group, and more testing is required in other areas and other taxa to confirm the generality of this conclusion.

The definition of targets is a crucial step in systematic conservation planning as they are used to define the conservation objective. Some authors have demonstrated that, to avoid inconsistent

solutions in selecting a reserve network, the targets need to consider at least 10% of each species' range (Levin et al. 2015). Other studies have used flexible targets depending on the global ranges extent, with a minimum 10% of the global range (Rodrigues et al. 2004; Di Marco et al. 2016). Criterion E is based on absolute targets that in proportion represents a very small species' range percentage. Targets described in Criterion E should ensure that sites selected under this Criterion contribute significantly to the global persistence of biodiversity. We consider that more testing is required to evaluate the effect of targets in the KBAs identification. First, it is necessary to evaluate how the current targets perform in other geographical regions and taxa. Second, testing how proportioned targets could fit in the identification of KBAs.

The current formulation of Criterion E is affected by the geographical scale and the application region, which means there is a risk of creating inconsistencies in the KBAs network (Baisero et al. 2022). The irreplaceability calculation at the country level seems to be largely influenced by restricted-range and endemic species, in the case of mammals, likely identifying similar sites to those identified by KBAs Criterion B, which considers geographically restricted species. Moreover, the results may differ depending on the stakeholder geographical level, supranational national or subnational. Having robust and standardised results is crucial for the KBAs identification process, which means that it is essential that stakeholders apply the KBAs Standard consistently. Therefore, the KBAs Guidelines must fix the application scale to avoid possible inconsistencies among different end-users identifying KBAs. Moreover, we recommend that to capture all potential irreplaceable sites, the preferent scale is set at a supranational level, e.g. continual level.

Currently, the KBAs Standards and Appeals Committee is updating the Guidelines for using *A global standard for the identification of Key Biodiversity Areas* (KBAs Standards and Appeals Committee 2020). While the current formulation of Criterion E captures some of the irreplaceable sites contributing significantly to the global persistence of biodiversity, there is potential to reformulate the Criterion to capture species richness independently of the scale, for example, adding proportional targets. The KBAs Standards and Appeals Committee can take some actions to make the analysis more robust. A starting point could be to set the scale of application at the regional level to reduce omission errors and ensure consistency. In the future, we consider that a revision of the targets would be valuable. However, more testing is required, including evaluating the use of proportional versus absolute targets and the effect in different geographical regions and taxa.

CHAPTER 5
GENERAL DISCUSSION

5.1 Key findings

This PhD is entitled Where will further Key Biodiversity Areas be identified? A modeling approach to focus efforts, however, the analysis developed on it goes beyond the KBA and focuses on those aspects that could improve the identification of KBA as a whole. This PhD is divided into three research papers aimed at improving, facilitating and standardizing the KBAs identification process. In the first two research papers (chapters two and three), I worked on improving accurate, high-quality AOH maps to identify KBAs. In the last (chapter four), I used these data to develop guidelines on the geographical scale of applicability of Criterion E from the KBAs Standard.

The production of AOH maps has traditionally been done using expert opinion to link habitat classes to land-cover types. In the first research chapter, I improved this method by modelling the relationship between the IUCN Habitat Classification Scheme and two widely used global land-cover maps, the Copernicus Global Land Service Land Cover (CGLS-LC100) and the European Space Agency Climate Change Initiative land cover 2015 (ESA-CCI). I generated two translation tables, quantifying the strength of association between habitat and land-cover classes using the odds ratio values of a logistic regression model. The results showed that some habitat classes (e.g. *forest* and *desert*) could be more confidently assigned to land-cover classes than others (e.g. wetlands and artificial). I calculated the association between habitat classes and land-cover classes as a continuous variable, allowing greater flexibility in using the results and removing the subjectivity inevitably associated with expert-driven methods. However, for producing the AOH maps it is necessary to establish a threshold of association, to transform the results into a binary table. The user could decide this threshold according to the required balance between omission and commission errors. I compared the performance of the data-driven models with expert knowledge, and they performed equally well, but the model provided greater standardization, objectivity, repeatability and allowed uncertainty to be quantified.

In the second research chapter, I developed AOH maps for 5,481 terrestrial mammals and 10,651 terrestrial bird species. For 1,816 bird species defined by BirdLife International as migratory, I

developed three AOH maps, one for the resident range, one for the breeding range and one for the non-breeding range. The maps have a resolution of 100 m. On average, AOH covered 66±28% of the range maps for mammals and 64±27% for birds. I used AOH maps to produce global maps of the species richness of mammals, birds, globally threatened mammals and globally threatened birds. These maps represent an increase in resolution compared with species richness maps produced using the IUCN range maps.

In the third data chapter, I evaluated the effect of the geographical scale on the application of Criterion E, which relates to irreplaceability. Irreplaceability is sensitive to the number of planning units considered in the analysis, and the biodiversity features include, therefore, the geographical scale and species inclusion affect the values and distribution of irreplaceability. These results indicated that at the regional level, irreplaceability is driven by endemic species and species complementarity, while at the country level, exclusively by endemic species. This indicates that calculating irreplaceable at the country level could underestimate the potential KBAs qualifying under Criterion E. Moreover, in the countries with few restricted-range species, the solution of the conservation problems returns seemingly random results as the ratio target/AOH is deficient. This information is critical to help understand how irreplaceability responds in the context of KBAs and establish mechanisms to make this Criterion more robust.

5.2 PhD Relevance in the context of KBAs

KBAs are an important tool for effective area-based conservation, and improving and supporting the identification of new KBAs are vital for stemming biodiversity loss. The identification of KBAs are at the interface of policy and science and stresses the importance of linking conservation science and conservation action. The three research papers in this PhD are an attempt to support the identification of KBAs through novel modelling methodologies of the different components of the KBAs identification process.

Data availability, quality, and bias are common challenges for biodiversity conservation (Meyer et al., 2015; Rondinini et al., 2006), so they also affect KBAs identification. Data availability differs between taxonomic groups and geographic regions, limiting the identification of KBAs (Maxwell et al. 2018). Therefore, improving data availability, accessibility, and accuracy is crucial for KBAs identification. AOH is one of the assessment parameters proposed in the Standard KBAs to apply the criteria and thresholds of KBAs identification. AOH will generally reduce the risks of commission error of range maps, and it is more available than other assessment parameters such as

Area of Occupancy (AOO) or the number of mature individuals. Improving the accuracy and accessibility of the AOH, therefore, directly impacts the identification of KBAs.
The data-driven translation table presented in the first research chapter is a method to improve the accuracy of AOH because it objectively removes unsuitable areas from the range map based on the information from the IUCN Habitat Classification Scheme. Our data-driven approach removes the expert-knowledge approaches' subjectivity. Moreover, this methodology can be used for other applications requiring translation between habitat and land cover. Habitat is the primary driver of biodiversity loss in the terrestrial realm; therefore, understanding its distribution is critical for biodiversity conservation.

AOH maps produced in the second research chapter have many other conservation applications (Brooks et al. 2019; Hanson et al. 2020a; Strassburg et al. 2020) beyond serving as an assessment parameter to identify KBAs (IUCN 2016). The status and trends of species' distributions are directly related to species' ecological conditions, population size, and extinction risk and are thus central to the conservation and management of species and their ecological functions (Oliver et al. 2021). AOH can assess species' distributions and monitor habitat loss and fragmentation, be used to estimate the rates of population decline under some of the Red List Criteria, and represent accurately systematic conservation planning analysis. Moreover, the richness maps derived from the AOH can help identify biodiversity hotspots accurately.

The KBAs criteria have quantitative thresholds to ensure that site identification is transparent, objective and repeatable. Therefore, the KBAs Standard must be robust against the scale and region of application. In the third data chapter, I demonstrated that the current formulation of Criterion E is not robust to the geographical scale and the application region, and when these parameters are modified the number and distribution of irreplaceable planning units differ. The KBAs Standards and Appeals Committee can take some actions to make the analysis more robust. A starting point could be to set the scale of application at the regional level to reduce omission errors and ensure consistency. In the future, a revision of the targets would be valuable.

5.3 Limitations and future work

In this PhD thesis, I presented several innovative methods that could help improve the identification and implementation of the KBAs and the data availability; however, further work could be developed to automatize the production AOH maps, reduce taxonomical bias, and make the Criterion more robust.

The first research chapter presents the relation between IUCN habitat and land-cover classes as a continuous variable showing a more realistic relationship between habitat and land cover and allowing end-users to decide the level of omission and commission errors. However, it is challenging to determine commission and omission errors as it requires presence and absence data, and absence data is rarely available (Boitani et al. 2011) . For that reason, an interesting continuation of the present work would be to evaluate the translation table with a set of independent presence-absence data. The analysis should be done in a region with heterogenic land cover classes and species with different habitat associations. Using the translation table, it is possible to set different association thresholds and obtain a range of binary, association-non-association, tables. Then, each table could be validated, and a confusion matrix built. The confusion matrix could be used to calculate different validation metrics such as overall accuracy, sensitivity and specificity. The end-users can use this metric to decide which threshold of association is the most convenient for their study.

Over time, the association between land cover and habitat will change because the three data sources used to produce the translation table will improve-data changes. There are annual updates for most land cover maps, and new products with higher accuracy are published frequently (Grekousis et al. 2015) . The current version of the IUCN Habitat Classification Scheme is described as a draft version (IUCN 2012); with the final version, some of the habitat definitions may change, modifying the species associated with the habitat. Moreover, with better knowledge, the habitat associations of different species may change. Finally, citizen science increases rapidly, and taxonomic and geographic bias may be reduced with this increase. A less biased point locality dataset would produce a more accurate and reliable translation table. The approach presented has the advantage that it can be adapted to develop a translation table between any set of habitat codes for any set of species and any set of land-cover classes at a global or regional scale; however, the automatization of the process can help to make the approach more accessible. The first step of the automatization would consist in downloading the new datasets. R packages for the three data sources could help automate the process: rgbif, for point locality, rredlist, for IUCN Red List assessments, and RCGLS, for Copernicus Land cover maps. The next step would be to clean point locality data; this is crucial to remove potential errors from the data set. We should then extract the land-cover class at each point locality, match it to the IUCN habitat class or classes assigned to each species occurring there, and model each land-cover class as a function of IUCN habitat. The code used for the present work could be used as a basis for this automatization. The code will be published with the article for this chapter.

Much work also remains on the automatization of AOH maps updates. Species on the Red List are re-evaluated, and range maps are updated when new information is available; therefore, the AOH should be updated at each modification of the range maps (IUCN 2019). This process could be done simultaneously with the automatization of the translation table. To update the AOH, it is necessary to obtain the range maps. Currently, there are no automatized ways to download the range. They must be downloaded manually from the IUCN Red List (https://www.iucnredlist.org/) or BirdLife International (http://datazone.birdlife.org) websites. One of the main challenges of the production of AOH is that it requires a logistic effort to have the computation power and the data storage necessary to make the updates. I recommend using GRASS-GIS software to reduce the computational cost, as it is more efficient in processing large amounts of raster data. Using GRASS-GIS, it is possible to adapt the code presented in the second research chapter to produce an updated set of AOH maps.

The taxa used in this thesis have been limited to terrestrial vertebrates for the first research chapter, terrestrial mammals and birds for the second research chapter and only terrestrial mammals for the third research chapter. These taxa are also the most well studied. Research is generally biased towards vertebrate taxa, especially mammals and birds (Di Marco et al. 2017a). However, having more accessible data has allowed me to focus on developing methodologies. Much work remains to assess the applicability of both AOH and KBAs to species beyond terrestrial vertebrates (Brooks et al. 2019). The current methodology of the AOH has not been applied to invertebrates, plants or outside the terrestrial realm, as more testing is required to understand how the IUCN habitat responds to these taxa. On the contrary, much work has been done to identify KBAs in the marine realm (Handley et al. 2020; Beal et al. 2021), but less effort for invertebrates, except for butterflies (Eken et al. 2016; Plumptre et al. 2019). However, more work is still necessary to develop the entire KBAs network that represents biodiversity with all its components and is free from taxonomical and geographical biases.

In Systematic Conservation Planning, targets describe the conservation objective. For some regions, the identification of KBAs using Criterion E targets analysis produced very few or no highly irreplaceable sites. However, it is unknown if this is a consequence of not having significant sites for the global persistence of biodiversity or if targets are deficient. This limits the use of Criterion E in most areas of the world. It is essential that the work on Criterion E continues, and more test is done to develop this Criterion to its whole (Baisero et al. 2022). The testing would require evaluating the use of proportional versus absolute targets and the effect in different

geographical regions and taxa. Also, it is important to evaluate the effect of using other taxa, especially taxa with more limited spatial distribution than mammals. In this thesis, I proposed that the irreplaceability analysis is run at a supranational level, however, it is acknowledged that increasing the scale of the analysis could limit the use of the criteria as it requires higher computational power.

5.4 Concluding remarks

The objective of this PhD is to standardize, improve and facilitate the process of KBAs identification which is crucial for effective area-based conservation. The translation table was developed to standardize the habitat and land cover relationship and the production of AOH maps. AOHs are an objective method to map species distributions and identify KBAs, homogenizing and reducing commission errors. These maps represent an improvement from previous versions of the AOH maps as they have a higher resolution and have been independently validated. The AOH maps are stored in an open access repository allowing free and immediate access. The evaluation of the effect of the geographical scale in the use of Criterion E helped standardise and clarify the guidelines for identifying KBAs. From the results of this analysis, I concluded that the current formulation of the Criterion is highly affected by the geographical scale, therefore, I proposed a set of measures to standardize and facilitate the use of this Criterion. I expect that the research carried out in this PhD constitutes an advance of the current knowledge on KBAs and serve as a starting point for future developments.

CHAPTER 6
OUTPUT AND CONTRIBUTIONS

6.1 Key research outputs

Lumbierres, M., Dahal, P. R., Di Marco, M., Butchart, S. H., Donald, P. F., & Rondinini, C. (2021). Translating habitat class to land cover to map area of habitat of terrestrial vertebrates. Conservation Biology.

Lumbierres, M., Dahal, R.P., Soria, C., Di Marco, M., Butchart, S.H.M., Donald, F.P., Rondinini, C. Area of Habitat maps for the world's terrestrial birds and mammals (under review)

Lumbierres, M., Narnia D., Schuster, R., Butchart, S. H., Donald, P. F., Di Marco, M. & Rondinini, C. Evaluating the use of Irreplaceability to identify Key Biodiversity Areas, and the effects of the geographical scale (in preparation)

6.2 Collaborative research outputs

Dahal, P. R., **Lumbierres, M.**, Butchart, S. H., Donald, P. F., & Rondinini, C. (2021). A validation standard for Area of Habitat maps for terrestrial birds and mammals. Geoscientific Model Development Discussions, (under review)

Dahal, P. R., **Lumbierres, M.**, Jung, M., Visconti, P., Butchart, S. H., Donald, P. F., & Rondinini, C. Comparison of Area of Habitat maps for terrestrial birds and mammals produced from habitat-land cover models and from a global map of terrestrial habitat classes. (in preparation)

Nania, D., **Lumbierres, M.**, Falaschi M., Ficetola G. F., Pacifici M., & Rondinini, C. Testing Key Biodiversity Areas Criteria through a Moving Window Approach on the Herpetofauna of Italy. (in preparation)

Nania, D., **Lumbierres, M.**, Falaschi M., Ficetola G. F. & Rondinini, C. Global Area of Habitat Maps for the Herpetofauna of Italy (in preparation)

Pacifici M., Cristiano A., **Lumbierres M.**, Dahal R. D., Belant J., Lucherini M., Mallon D., Meijaard E., Solari S., Tognelli M., Butynski T., Cronin D., d'Huart J.P., de Jong Y., Dheer A., Fei L., Gallina S., Goodrich J., Harihar A., Hewitt D., Lopez Gonzalez C., King S., Lewison R., Melo F., Napolitano C., Robinson P., Semiadi G., Strier K., Talebi M., Taylor A., Ting N., Thiel-Bender C., Wiesel I., Rondinini C. Recent changes in area of habitat to identify priority areas for conservation interventions for mammals (in preparation)

Kim H., Bae S., Chaplin-Kramer R., **Lumbierres M.**, Ferrier S., Garnett S., Meyer C., Molnár Z., Quoß L., Remelgado R., Rondinini C., Sharp R., Pereira H. Nature Futures retrospective analyses on the impact of protected areas on biodiversity and ecosystem services using the essential biodiversity 2000-2018 (in preparation)

6.3 Report participation

KBAs Standards and Appeals Committee (2020). Guidelines for using A Global Standard for the Identification of Key Biodiversity Areas. Version 1.1. Prepared by the KBAs Standards and Appeals Committee of the IUCN Species Survival Commission and IUCN World Commission on Protected Areas. Gland, Switzerland: IUCN. viii + 206 pp.

6.4 Conferences contributions

IBS 2019 International Biogeography Society Humboldt Meeting, Quito, Ecuador. Poster: Modelling habitat-land cover associations for mapping species distributions: Methods. August 2019

ISEM 2019 International Society for Ecological Modeling Global Conference, Salzburg, Austria. Poster: Modelling habitat-land cover associations for mapping species distributions. October 2019

GEOBON Open Science Conference & All Hands Meeting, Online. Oral presentation: Updated Area of Habitat models to map global biodiversity for terrestrial mammals and birds. July 2020

ASM 2021 100th Annual Meeting of the American Society of Mammologists Symposium: ASM Global trends in mammal distribution and threats Oral presentation: Global patterns of mammals distribution based on new set of Area of Habitat maps. June 2021

ICCB 2021 30th International Congress for Conservation Biology Online Oral presentation: Evaluating Irreplaceability in Key Biodiversity Areas and the effects of the geographical scale. December 2021

SCCS 2022 Student Conference on Conservation Science. Cambridge, UK, Poster: Area of Habitat maps for the world's terrestrial birds and mammals. March 2022

6.5 Secondments

BirdLife International Cambridge, UK. January 2019 - May 2019.

6.6 Coursers

Key Biodiversity Areas Identification Training, Dr Andy Plumtree and Dr Penny Langhammer. Rhodes, April, 2019

Summer School on spatial and spatiotemporal computing: processing large-scale Earth observation data. Opengeohub, University of Münster, September 2019

IUCN Red List Assessor Training, IUCN, Catherine Sayer and Federica Chiozza. Rome October 2019

Hints and Tips for publishing in ecology and conservation. Dr Moreno di Marco, Sapienza University of Rome, February 2020

Grant writing and career perspective, Dr Moreno di Marco, Sapienza University of Rome, February 2020

Palaeoecology and climate change. Dr Donatella Magri, Sapienza University of Rome, July 2020

Introduction to SDMs: theory and practice in R, Dr Robert Muscarella, Sapienza University of Rome, June 2021

Theory and practice of communicating at the science-policy interface, Inspire4 Nature training, Dr. Ana Rodrigues. Online July 2021

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SUPPLEMENTARY MATERIAL

Supplementary material Chapter 2

Appendix S2.1 IUCN habitat description

IUCN habitat definitions included in the modelling of habitat land-cover associations. Definitions derived for the IUCN Habitat Classification Scheme and Ramsar

IUCN Code	IUCN Habitat class definition
H1	**Forest:** Forest consists of a continuous stand of trees and includes both forested areas (generally with a closed canopy) and wooded areas.
H2	**Savanna:** Savannas are transitional between grasslands and forests. They are ecosystems dominated by a grass ground cover with an overstorey of widely spaced trees and shrubs.
H3	**Shrubland:** Also referred to as scrub, bushland and thicket.
H4	**Grassland:** Native grasslands are comprised of grasses and broadleaved herbaceous plants, and are either without woody plants, or the latter are very sparsely distributed.
H4	**Grassland:** Native grasslands are comprised of grasses and broadleaved herbaceous plants, and are either without woody plants, or the latter are very sparsely distributed.
H5	**Wetlands:** Areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters.
H6	**Rocky Areas:** cliffs, mountain peaks, talus, feldmark.
H8	**Desert:** Consists of arid landscapes with a sparse plant cover, except in depressions where water accumulates. The sandy, stony, or rocky substrate contributes more to the appearance of the landscape than does the vegetation.
H14.1 H14.2	**Artificial arable and pasture lands:** 14.1 Arable Land Includes cereal fields, rice paddies, perennial crops, orchards and groves. 14.2 Pastureland Includes fertilized or re-seeded permanent grasslands, sometimes treated with selective herbicides, with very impoverished flora and fauna. Also includes secondary grasslands and wooded farmland.

H14.3 H14.6	**Artificial degraded forest and plantation:** 14.3 Plantations: A plantation is an intentional planting of a crop, on a larger scale, usually for uses other than cereal production or pasture. The term is currently most often used for plantings of trees and shrubs. The term tends also to be used for plantings maintained on economic bases other than that of subsistence farming. 14.6 Subtropical/Tropical Heavily Degraded Former Forest: Former subtropical or tropical forest that has been extensively cleared or impacted by human activities. Often there is some degree of regeneration or there are small fragments of forest remaining.
H14.4 H14.5	**Artificial urban and rural gardens:** 14.4 Rural Gardens: Rural gardens are located in a rural setting, serving families whose main income comes from wage labor (rural or urban). Rural gardens differ from arable land production by the following features which are usually, but by no means in all cases, found simultaneously: (1) cropping plants for personal consumption that cannot be collected nor supplied by arable farming, (2) small plots, (3) proximity to the house, (4) fencing, (5) mixed or dense planting of a great number of annual, semi-permanent, and perennial crops, (6) a high intensity of land use, (7) land cultivation several times a year, (8) permanence of cultivation, and (9) cultivation with hand implements. 14.5 Urban Areas Usually metropolitan and commercial areas dominated by asphalt, concrete and roof. Includes buildings, lawns and parks.
H.15	**Artificial Aquatic:** These are human-made wetland habitats.

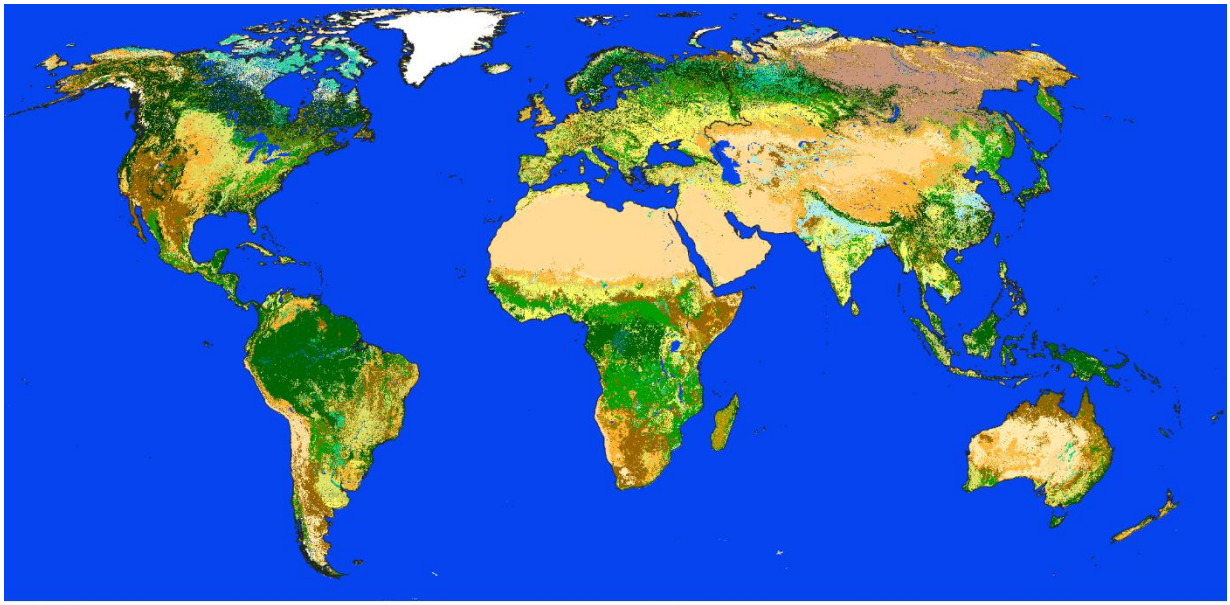
Appendix S2.2 links to downloaded figure 4

Figure 4 can be downloaded in geotiff format at:

Lumbierres, Maria. (2021). Map of habitat classes (Level 1) from the IUCN Habitat. Zenodo. https://doi.org/10.5281/zenodo.5146073

Appendix S2.3 Map of habitat classes derived from ESA-CCI

Map of habitat classes (Level 1) from the IUCN Habitat classification scheme based on the middle threshold for ESA-CCI data-derived translation.



- *Forest*
- *Forest, Rocky areas*
- *Forest, Savanna, Shrubland, Wetlands, Artificial urban areas and rural gardens*
- *Savanna, Shrubland, Grassland, Rocky areas, Artificial Aquatic*
- *Savanna, Shrubland, Grassland, Wetlands, Artificial arable and pasture lands, Artificial urban areas and rural gardens, Artificial Aquatic*
- *Savanna, Grassland, Wetlands, Artificial arable and pasture lands, Artificial urban areas and rural gardens, Artificial Aquatic*
- *Savanna, Grassland*
- *Artificial degraded forest and plantation*
- *Grassland, Wetlands, Artificial arable and pasture lands, Artificial degraded forest and plantation, Artificial urban areas and rural gardens, Artificial Aquatic*
- *Savanna, Shrubland, Rocky areas, Desert*
- *Artificial arable and pasture lands*
- *Wetlands*
- *Forest, Wetlands*
- *Grassland*
- *Savanna, Shrubland, Grassland, Rocky areas, Desert*
- *Forest, Wetlands, Artificial Aquatic*
- *Wetlands,Artificial Aquatic*
- *Savanna, Wetlands, Artificial Aquatic*
- *Artificial arable and pasture lands, Artificial degraded forest and plantation, Artificial urban areas and rural gardens, Artificial Aquatic*
- *Shrubland, Grassland, Rocky areas, Desert*
- *Wetlands, Artificial urban areas and rural gardens, Artificial Aquatic*

Supplementary material Chapter 4

Appendix S4.1 Density models to establish the targets the "area necessary to include 1,000 mature individuals"

We use a linear mixed-effects model, lmer function from the lme4 R package (Bates et al., 2015). We modelled density for 1228 species of mammal that we had information on density, body mass and trophic level. We applied a log function to the density and body mass and added order as a random effect (eq1, table 2)

$$eq1. log(density)\ log(adultmass) + trophic_{level} + (1 \vee order) - 1$$

Table 1: Density model summary

```
Scaled residuals:
   Min      1Q  Median      3Q     Max
-4.1436 -0.6325 -0.0125  0.6633  3.2126

Random effects:
 Groups   Name        Variance Std.Dev.
 order    (Intercept) 1.254    1.120
 Residual             2.695    1.642
Number of obs: 1228, groups:  order, 22

Fixed effects:
                 Estimate Std. Error t value
log(adult_mass_g) -0.55391    0.03241  -17.09
trophic_level1     7.94772    0.38927   20.42
trophic_level2     7.39506    0.36193   20.43
trophic_level3     6.89953    0.36993   18.65

Correlation of Fixed Effects:
            lg(__) trph_1 trph_2
trophc_lvl1 -0.665
trophc_lvl2 -0.601  0.951
trophc_lvl3 -0.556  0.837  0.856
```

Once we obtained the model's coefficients, we predicted density information for 4263 species of mammals with information on body mass and trophic level but not information on density. From 5791 species of mammals in total, 219 had a density higher than one individual square kilometre.

Appendix S4.2 Statistical test comparing the planning units characteristics

Statistical test comparison, ANOVA and Tukey multiple pairwise comparisons among the three groups of planning units in South America. Group 1 planning units selected in the regional analysis, group 2 planning units selected in the country-level analysis, and group 3 planning units not selected

Table 2: Number of species per planning unit one-way ANOVA test among the three groups of planning units in South America

	Colombia					Ecuador				
	DF	Sum Sq	Mean Sq	F Value	P	DF	Sum Sq	Mean Sq	F Value	P Value
N sp	2	30602	15301	55.18	**<2e-16**	2	121386	60693	50.26	**<2e-16**
	Peru					**Venezuela**				
N sp	2	599894	299947	70.01	**<2e-16**	2	22849	11425	54.61	**<2e-16**

Table 3: Number of species per planning unit Tukey multiple pairwise-comparisons among the three groups of planning units in South America

	Colombia				Ecuador			
	Diff	Lwr	Upr	P adj	Diff	Lwr	Upr	P adj
2-1	7.559524	3.652972	11.466075	**1.73e-05**	32.571165	23.190181	41.95215	**0.0000000**
3-1	-4.82917	-7.34489	-2.313454	**2.05e-05**	4.141283	-2.777438	11.06000	0.3391136
3-2	-12.3886	-15.4225	-9.354865	**0.00e+00**	-28.42988	-35.22107	-21.63869	**0.0000000**
	Peru				**Venezuela**			
2-1	45.41126	34.99922	55.82330	**0.0000000**	-22.63206	-29.39637	-15.86774	**0.0e+00**
3-1	3.91743	-2.64630	10.48116	0.3414538	-9.88655	-12.38475	-7.388352	**0e+00**
3-2	-41.4938	-49.8116	-33.17603	**0.0000000**	12.745508	6.439379	19.051637	**6.6e-06**

Table 4: Mean AOH area per planning unit one-way ANOVA test among the three groups of planning units in the South America

	Colombia					Ecuador				
	DF	Sum Sq	Mean Sq	F Value	P	DF	Sum Sq	Mean Sq	F Value	P Value
Mean size AOH	2	1.843e+12	9.216e+11	26.89	**2.24e-12**	2	3.981e+12	1.990e+12	59.03	**<2e-16**
	Peru					**Venezuela**				
Mean size AOH	2	1.838e+13	9.191e+12	51.87	**<2e-16**	2	2.422e+11	1.211e+11	24.12	**3.5e-11**

Table 5 Mean AOH area per planning unit Tukey multiple pairwise-comparisons among the three groups of planning units in the South America Tukey multiple pairwise-comparisons

	Colombia				Ecuador			
	Diff	Lwr	Upr	P adj	Diff	Lwr	Upr	P adj

2-1	58776.08	15343.568	102208.60	**0.0043291**	225957.56	176387.98	275527.13	**0**
3-1	85109.51	57140.113	113078.91	**0.0000000**	93318.79	56759.93	129877.64	**0**
3-2	26333.43	-7396.272	60063.13	0.1598435	-132638.8	-168523.8	-96753.79	**0**
	Peru				**Venezuela**			
2-1	241517.12	174557.62	308476.63	**0.0000000**	-38735.45	-71868.99	-5601.898	0.0169204
3-1	10022.33	-32188.82	52233.47	0.8431162	25885.75	13648.84	38122.660	**0.0000022**
3-2	-231494.8	-284986.3	-178003.3	**0.0000000**	64621.20	33731.97	95510.422	**0.0000029**

Appendix S4.3 Statistical test comparing the between study regions

Statistical test comparison, ANOVA and Tukey multiple pairwise among the countries of the two study regions, South America and East Africa.

Table 6: Stat metrics comparisons among the counties of the two study regions

Country	**% AOH inside the country**				**AOH size**				**Target/ AOH ratio**			
	Q.1	**Mean**	**Median**	**Q.3**	**Q.1**	**Mean**	**Median**	**Q.3**	**Q.1**	**Mean**	**Median**	**Q.3**
Colombia	0.298	0.488	0.386	0.725	1.6E+10	2.6E+11	1.2E+11	4.8E+11	0.001	0.063	0.002	0.013
Ecuador	0.060	0.243	0.098	0.254	1.6E+10	6.7E+10	5.7E+10	9.8E+10	0.001	0.051	0.002	0.010
Peru	0.321	0.604	0.547	1.000	1.1E+10	2.6E+11	1.1E+11	5.4E+11	0.001	0.087	0.004	0.027
Venezuela	0.205	0.441	0.302	0.762	2.8E+10	2.6E+11	2.0E+11	4.8E+11	0.001	0.051	0.002	0.006
Kenya	0.192	0.446	0.333	0.731	1.8E+10	1.4E+11	7.3E+10	2.2E+11	0.001	0.028	0.004	0.016
Uganda	0.078	0.285	0.155	0.422	1.1E+10	7.6E+10	5E+10	1.1E+11	0.001	0.015	0.003	0.012
South Sudan	0.096	0.339	0.290	0.512	1.8E+10	1.8E+11	7.5E+10	3.6E+11	0.001	0.011	0.002	0.008
Ethiopia	0.191	0.445	0.374	0.620	3.7E+10	2.4E+11	1.3E+11	3.5E+11	0.001	0.011	0.002	0.007

Table 7 % of the range inside a country comparison one-way ANOVA test among the countries of the two study regions, South America and East Africa

	DF	**Sum Sq**	**Mean Sq**	**F Value**	**P**
% Range inside the country	7	36.3	5.185	50.66	<2e-16

Table 8 % of the range inside a country Tukey multiple pairwise-comparisons among the countries of the two study regions, South America and East Africa

pairwise comparison	**diff**	**lwr**	**upr**	**p adj**
Kenya-Colombia	-0.0415	-0.1124	0.0295	0.6386
Kenya-Ecuador	**0.2027**	**0.1272**	**0.2783**	**0.0000**
Kenya-Peru	**0.1577**	**0.0868**	**0.2286**	**0.0000**
Kenya-Venezuela	-0.0057	-0.0810	0.0696	1.0000
Uganda-Colombia	**-0.2031**	**-0.2771**	**-0.1292**	**0.0000**

Uganda-Ecuador	0.0411	-0.0373	0.1194	0.7561
Uganda-Peru	**-0.3194**	**-0.3933**	**-0.2455**	**0.0000**
Uganda-Venezuela	**0.1560**	**0.0779**	**0.2341**	**0.0000**
South Sudan-Colombia	**-0.1491**	**-0.2262**	**-0.0720**	**0.0000**
South Sudan-Ecuador	**0.0951**	**0.0138**	**0.1765**	**0.0095**
South Sudan-Peru	**0.2654**	**0.1883**	**0.3425**	**0.0000**
South Sudan-Venezuela	**0.1020**	**0.0208**	**0.1831**	**0.0035**
Ethiopia-Colombia	-0.0430	-0.1207	0.0347	0.7003
Ethiopia-Ecuador	**0.2012**	**0.1193**	**0.2831**	**0.0000**
Ethiopia-Peru	**0.1593**	**0.0817**	**0.2370**	**0.0000**
Ethiopia-Venezuela	-0.0041	-0.0858	0.0775	1.0000

Table 9 *Mean range size per country comparison one-way ANOVA test among the countries of the two study regions, South America and East Africa*

	DF	**Sum Sq**	**Mean Sq**	**F Value**	**P**
Mean range size	7	1.628e+25	2.325e+24	46.52	<2e-16

Table 10 *Mean range size per country Tukey multiple pairwise-comparisons among the countries of the two study regions, South America and East Africa*

pairwise comparison	**diff**	**lwr**	**upr**	**p adj**
Kenya-Colombia	**-1.11244E+11**	**-1.60815E+11**	**-61673303668**	**0**
Kenya-Ecuador	**77211821052**	**24438940688**	**1.29985E+11**	**0.000253**
Kenya-Peru	**1.15207E+11**	**65656386079**	**1.64758E+11**	**0**
Kenya-Venezuela	**1.15308E+11**	**62704487871**	**1.67911E+11**	**1.06E-10**
Uganda-Colombia	**-1.80074E+11**	**-2.31721E+11**	**-1.28427E+11**	**0**
Uganda-Ecuador	8381776734	-46345949114	63109502582	0.999794
Uganda-Peru	**-1.84037E+11**	**-2.35665E+11**	**-1.32409E+11**	**0**
Uganda-Venezuela	**1.84138E+11**	**1.29574E+11**	**2.38702E+11**	**0**
South Sudan-Colombia	**-74675168355**	**-1.28569E+11**	**-20780865354**	**0.000715**
South Sudan-Ecuador	**1.13781E+11**	**56927674709**	**1.70634E+11**	**3.97E-08**
South Sudan-Peru	**78637901924**	**24762314814**	**1.32513E+11**	**0.000265**
South Sudan-Venezuela	**78738470013**	**22042794472**	**1.35434E+11**	**0.000686**
Ethiopia-Colombia	-13470581884	-67751483400	40810319632	0.995291
Ethiopia-Ecuador	**1.74986E+11**	**1.17766E+11**	**2.32205E+11**	**0**
Ethiopia-Peru	17433315452	-36829003516	71695634421	9.78E-01
Ethiopia-Venezuela	17533883541	-39529414632	74597181715	0.982976

Table 11 *Target/ AOH range ratio comparison one-way ANOVA test among the countries of the two study regions, South America and East Africa*

DF	Sum Sq	Mean Sq	F Value	P
7	1.90	0.27104	10.52	4.09e-13

Table 12 *Target/ AOH range ratio Tukey multiple pairwise-comparisons among the countries of the two study regions, South America and East Africa*

pairwise comparison	diff	lwr	upr	p adj
Kenya-Colombia	-1.11244E+11	-1.60815E+11	-61673303668	0
Kenya-Ecuador	77211821052	24438940688	1.29985E+11	0.000253
Kenya-Peru	1.15207E+11	65656386079	1.64758E+11	0
Kenya-Venezuela	1.15308E+11	62704487871	1.67911E+11	1.06E-10
Uganda-Colombia	-1.80074E+11	-2.31721E+11	-1.28427E+11	0
Uganda-Ecuador	8381776734	-46345949114	63109502582	0.999794
Uganda-Peru	-1.84037E+11	-2.35665E+11	-1.32409E+11	0
Uganda-Venezuela	1.84138E+11	1.29574E+11	2.38702E+11	0
South Sudan-Colombia	-74675168355	-1.28569E+11	-20780865354	0.000715
South Sudan-Ecuador	1.13781E+11	56927674709	1.70634E+11	3.97E-08
South Sudan-Peru	78637901924	24762314814	1.32513E+11	0.000265
South Sudan-Venezuela	78738470013	22042794472	1.35434E+11	0.000686
Ethiopia-Colombia	-13470581884	-67751483400	40810319632	0.995291
Ethiopia-Ecuador	1.74986E+11	1.17766E+11	2.32205E+11	0
Ethiopia-Peru	17433315452	-36829003516	71695634421	9.78E-01
Ethiopia-Venezuela	17533883541	-39529414632	74597181715	0.982976

Appendix S4.4 Representation of Ecuador, Peru and Venezuela targets multiplied 2, 5, and 10

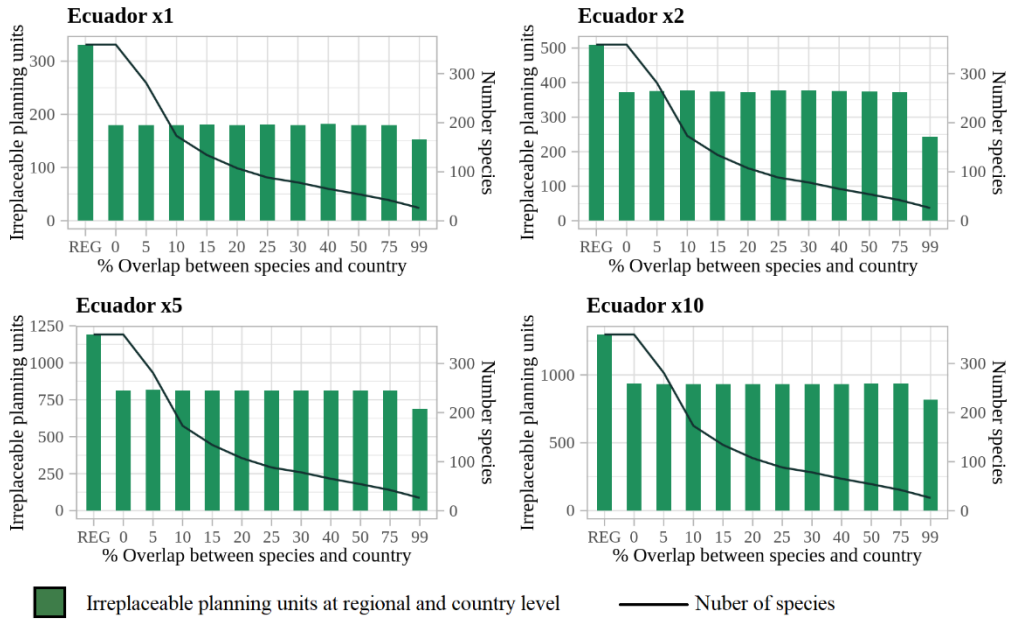


Figure S4.1 Number of planning units in Ecuador with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds

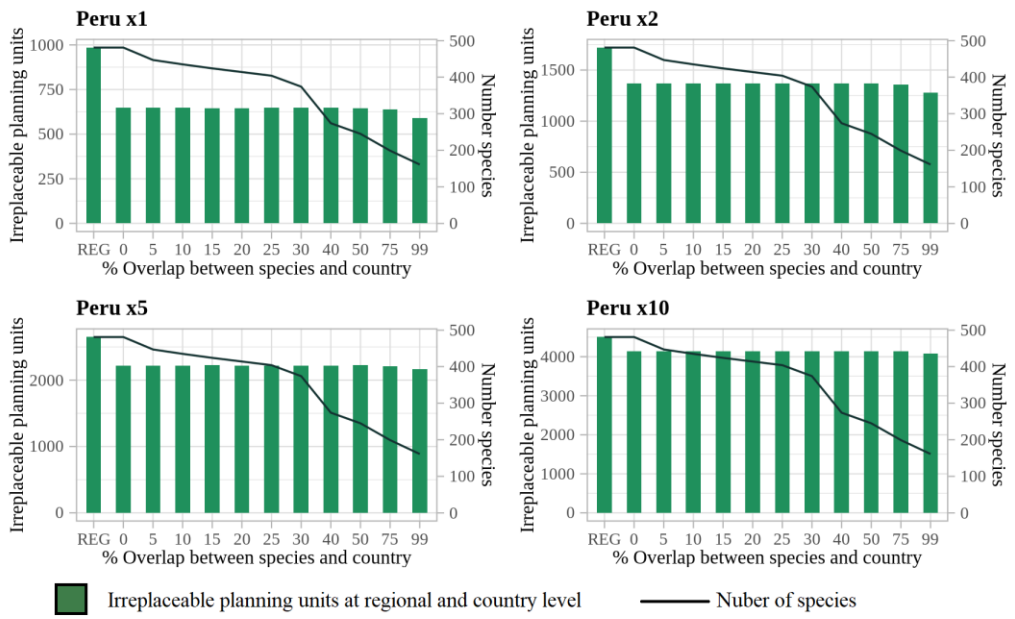


Figure S4.2 Number of planning units in Peru with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds

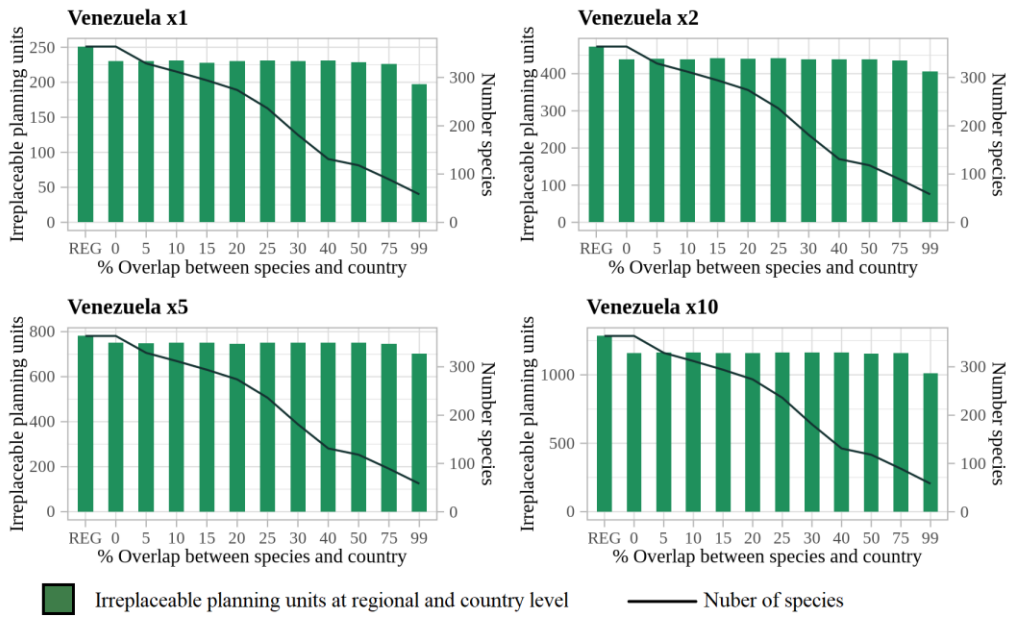


Figure S4.3 Number of planning units in Venezuela with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds

Appendix S4.5 Representation of Kenya, Uganda, and South Sudan targets multiplied 2, 5, and 10

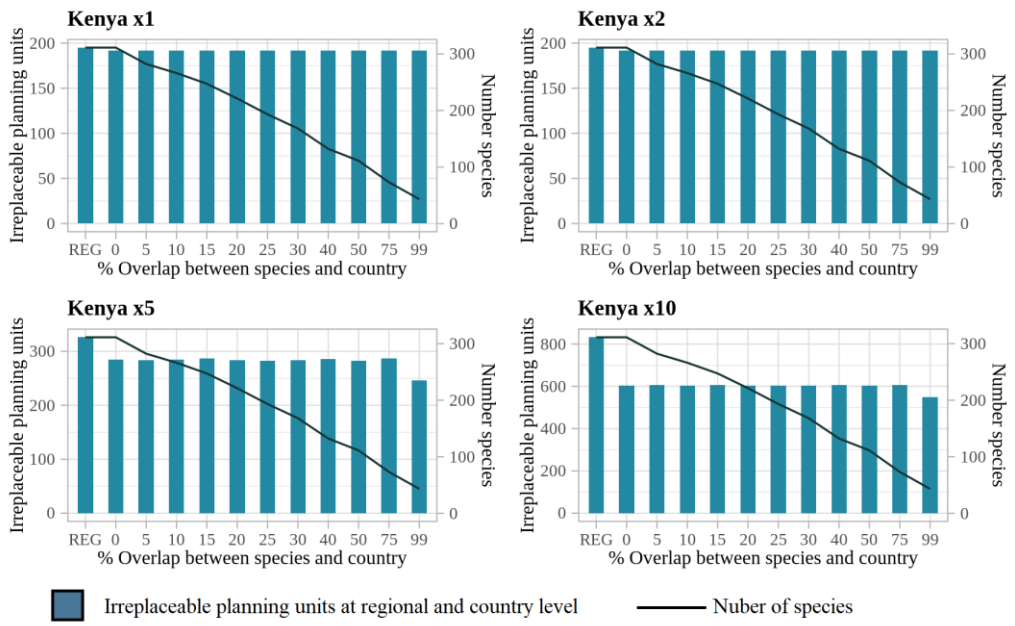


Figure S4.4 Number of planning units in Kenya with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2,

5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds

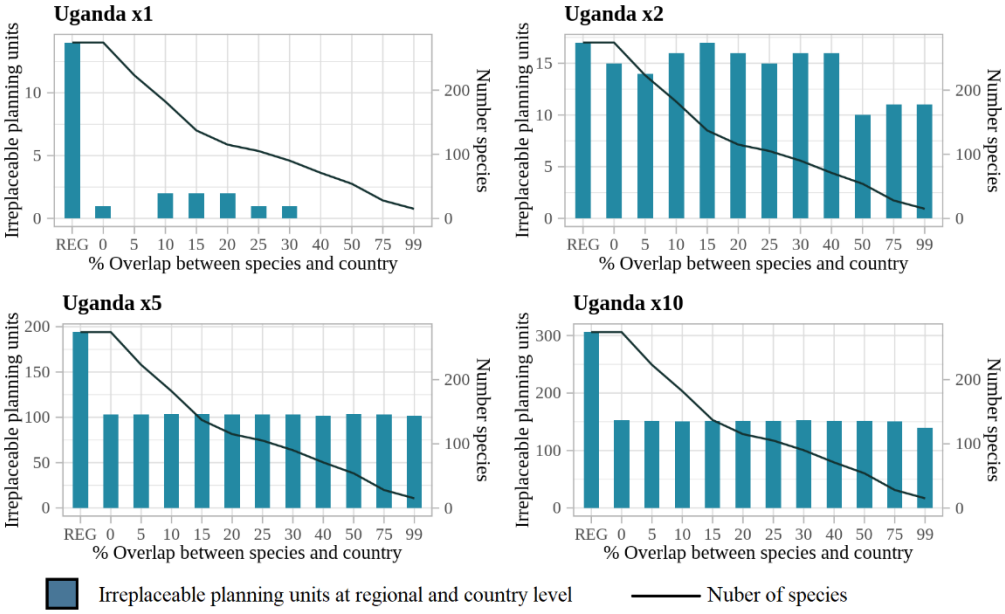


Figure S4.5 Number of planning units in Uganda with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds

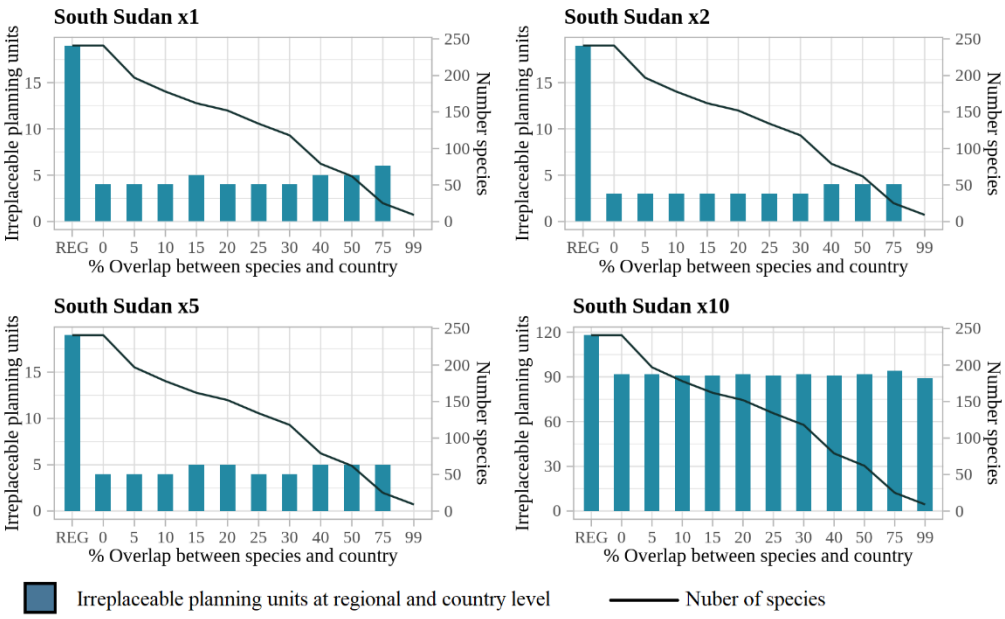


Figure S4.6 Number of planning units in Sauth Sudan with irreplaceability higher than 0.9, calculated using Marxan selection frequency with the targets set in the KBAs Standard, and with targets multiplied by 2, 5, and 10. The first column of each graph represents the regional-level analysis and the rest of the columns the country-level analysis with different species inclusion thresholds