Advancing the use of Evolutionary Considerations in Spatial Conservation Planning

Stuart Robertson

This thesis is submitted to the School of Science, Engineering and Environment, University of Salford, in fulfilment of the requirements for the degree of Doctor of Philosophy

2020

Supervisory team:

Dr. Katherine Yates, Dr. Robin Beck, University of Salford, Manchester

Professor Stefano Mariani, Liverpool John Moores University, Liverpool

TABLE OF CONTENTS

TABLE OF CONTENTS I

LIST OF FIGURES V

LIST OF TABLES VII

ACKNOWLEDGEMENTS VIII

ABSTRACT IX

CHAPTER 1 INTRODUCTION 1

1.1 Spatial conservation planning..3

1.2 Evolutionary considerations 4

1.3 Aims and approach: 6

CHAPTER 2 THE INCLUSION OF PHYLOGENETIC DIVERSITY WITHIN OPTIMISED SPATIAL CONSERVATION PLANNING –THE STATE OF THE ART 8

2.1 Introduction 8

2.1.1 Phylogenetic diversity and spatial conservation planning..8

2.2 Method 11

2.3 Results..13

2.4 Discussion..20

2.4.1 Incorporating PD 21

2.4.2 Spatial optimisation tools..23

2.4.3 Scale 25

2.4.4 Spatial patterns of PD Vs priority areas for conservation..25

2.4.5 Spatial mismatches between priority areas for PD and species richness..26

2.4.6 Surrogacy..27

2.4.7 Underrepresentation of PD within existing protected areas..28

2.4.8 Functional diversity 29

2.5 Conclusion..29

CHAPTER 3 CONSERVING THE PRIMATE TREE OF LIFE: PHYLOGENETIC DIVERSITY-BASED CONSERVATION PLANNING REVEALS SPATIAL MISMATCHES WITH A SPECIES-BASED APPROACH AS WELL THE POTENTIAL FOR SPECIES RICHNESS TO ACT AS A SURROGATE METRIC FOR PHYLOGENETIC DIVERSITY 32

3.1 Introduction 32

3.2 Methods 35

3.2.1 Spatial data 35

3.2.2 Phylogenetic data 36

3.2.3 Branches as conservation features 36

3.2.4 Target setting 38

3.2.5 Spatial optimisation 38

3.2.6 Species-based approach 39

3.3 Results 41

3.4 Location of priority areas 41

3.5 Amount of PD captured 44

3.6 Discussion 47

3.6.1 Spatial mismatches 47

3.6.2 Species as a surrogate for PD 50

CHAPTER 4 OPTIMISING THE SELECTION OF SPECIES TO MAXIMISE PHYLOGENETIC DIVERSITY PROVIDES A NEW APPROACH FOR PHYLOGENETICALLY-INFORMED SPATIAL CONSERVATION PLANNING 53

4.1 Introduction 53

4.2 Methods 57

4.2.1 Data 57

4.2.2 Gridding and MARXAN databases/input files 57

4.2.3 Using Phylogenetic Diversity Analyzer (PDA) 58

4.2.4 Running MARXAN 59

4.2.5 Set selection 61

4.2.6 Binning branches 61

4.3 Results 63

4.4 Discussion 69

CHAPTER 5 “SPLITTING” VS "LUMPING" AND PHYLOGENETIC DIVERSITY: THE IMPACT OF TAXONOMIC CHANGES ON THE SPATIAL CONSERVATION OF EVOLUTIONARY HISTORY 77

5.1 Introduction 77

5.2 Methods 80

5.2.1 Split and Lumped trees 80

5.2.2 Species range data 81

5.2.3 Optimising selection of species 81

5.3 Results 84

5.4 Discussion 90

CHAPTER 6 DISCUSSION 96

6.1 General Discussion 97

6.1.1 The emerging field of PD-informed conservation 98

6.1.2 A novel weighted branch-based approach for incorporating PD into spatial conservation planning 99

6.1.3 Is species richness an effective surrogate for PD? 100

6.1.4 A new approach 102

6.1.5 The impact of changes in species-level taxonomy on conservation planning 102

6.1.6 The potential for incorporating alternative metrics into spatial conservation planning 104

6.1.7 Concluding remarks 106

APPENDIX 108

I.) Every tip per node 108

II.) Get unions from every tip per node 109

III.) Create MARXAN species file for every set 110

IV.) MARXAN Loop for sets 111

REFERENCES 112

LIST OF FIGURES

Figure 1.1 Generalised phylogenetic tree, depicting the most important tree elements. 5
Figure 2.1 The number of studies published each year that have included "Phylogenetic Diversity" AND "Conservation" within their title and/or abstract. 11
Figure 3.1 Breaking down the phylogeny of a clade. 40
Figure 3.2 Selection frequencies 42
Figure 3.3 Priority areas for conserving primate phylogenetic diversity and species richness (and the differences between the two) when the area available is limited to 2.5% of total primate range. 43
Figure 3.4 Priority areas for conserving primate phylogenetic diversity and species richness (and the differences between the two) when the area available is limited to 10% of total primate range. 44
Figure 3.5 The amount of PD (a) and number of species (b) captured by each approach 46
Figure 4.1 Workflow for a novel approach to incorporating phylogenetic diversity (PD) into spatial conservation planning. 63
Figure 4.2 The area required to protect different percentages (10-100% in 10% increments) of total Phylogenetic Diversity (PD) for the placental mammal orders Artiodactyla, Carnivora and Primates. 64
Figure 4.3 Boxplots for species range within each order. 66
Figure 4.4 Boxplots for species richness within each order. 67
Figure 4.5 The amount of Phylogenetic Diversity (PD) captured by optimally selecting species for PD. 68
Figure 4.6 The composition of the phylogenetic trees for Artiodactyla, Carnivora, and Primates 69
Figure 5.1 Lumped and Split phylogenies. 83
Figure 5.2 The area required to protect Phylogenetic Diversity (PD) for African bovid species. 85
Figure 5.3 Selection frequencies for differing amounts of phylogenetic diversity (PD) for both trees, lumped and split. 87
Figure 5.4 Difference map for the selection frequency of MARXAN solutions conserving 90% PD (lumped minus split). 88
Figure 5.5 Violin boxplots for species ranges for each tree (lumped and split). 89

Figure 5.6 Violin boxplots for species richness for each phylogeny (lumped and split). 90

LIST OF TABLES

Table 2.1 The key words used iteratively in the structured review. 13

Table 2.2. A breakdown of the studies identified by the structured review, highlighting key information on methodologies and findings. 16

Table 4.1 Number of sets of species, as identified by Phylogenetic Diversity Analyzer (PDA), ... 62

ACKNOWLEDGEMENTS

What a mad journey. I am oh so grateful. For Katherine, at times I didn't think I'd get here, but your unwavering support and insight saw me through in good stead, thank you, so much. For Robin, a band mate, a quiz mate, a mate, a supervisor, your steady hand was essential, and not just for those Paul Kossoff-esque solos. For Stefano, your exuberance made starting off on this thing all the more exciting. For Silvia, thank you for your time, and your expertise, and for making my time at CIBIO fantastic; and thanks to all the CIBIO peeps. For Montmano, for Ais, Telle, and James. For the Bluedot and Latitude team. For Swithers, Lats, Goodface, Meg, and Sam, and the rest of the crew. For Andy, for the SciComm opportunities. For Natalie. For the Tardigrades, I assume we have a responsibility to headline all future SEE Christmas parties? For SPEC. For Club 110. For Rory, those hugs, my dude. Sam, you feature heavily in here, and I wouldn't have it any other way - we interviewed on the same day, started on the same day, and here we are 4 (and a bit) years later, handing in on *nearly* the same day. I think we deserve a drink, my friend. For José, take me back to Porto. For Ed, let's not wait another 20 years to have that next jam. For Rachel and 58008 (Robin you've already made a few appearances) what a legacy. For Benji, where *is* Becky by the way?(For Becky). For Alex, 12:30 lunch? For the Peel lunch club. For Richard, all that GIS paid off. For Paddy, I didn't think I would be mentioning Paul Kossof *twice* in my thesis, but there you go man. For Charles, it turns out you were right, R *is* better, but thank you also for your perspective on all *this*. For Doug, we dived on the Great Barrier Reef!-and for the Fizzy Cs. For Brian, for lake beers. For Gary, my Manc brother. For Mark, what a pairing. For Bess, and for Bermuda. For Ed, Mo, and Paul, thank you for being the best unexpected housemates and friends, and helping keep me sane these last months – and from Pierre, he looks forward to welcoming you into his palace once more. For Milo, medics, ey? For Edwin, for Campari. For Chris, mate, maaaaaaate, no but really, 21 years. For Sophie, babes, I did it!-you kept telling me I would. For Saskia. Sask, I honestly don't know what I would have done without you, and your love and support, no, but _*really though*_, thank you. For Donal. Anyone that is even the slightest bit aware of this thesis knows how important you are to it, and to me. Oh, and 'Donal Coffee!' – well that was set 1025 days ago. For Kelly, feels like this PhD has taken me abooouuut…10 hours? For Mum and for Dad, turns out if I just got my head down, it would get done. Thank you for believing in me.

- Right, 5pm, steps outside Peel? I'll meet yous there.

ABSTRACT

The existence of life on earth as we know it relies on a diversity of life. Biodiversity underpins vital ecosystems services globally, at all spatial scales, and yet is being lost at an alarming rate. Current extinction rates are estimated to be 100-1000 times higher than the typical background rates observed in the fossil record, with anthropogenic influences being the major driving force. It is therefore widely accepted that biodiversity must be protected. Spatial tools, such as protected areas, are increasingly employed to meet conservation objectives. Despite continuing developments in spatial conservation methods, a fundamental aspect of biodiversity remains largely ignored, namely evolutionary processes. Evolution is the process that generates and maintains biodiversity. However, examples of where evolutionary considerations have been explicitly incorporated into spatial conservation planning remain rare, with metrics such as species richness (which ignore differences in evolutionary distinctiveness between species) more often used. This work aims to address this by focusing on the inclusion of phylogenetic diversity (PD), which measures evolutionary diversity by summing the branch lengths joining a species, or set of species, into protected area planning. A review of the literature revealed that there has been a huge increase, an average 80% increase per year in the last five years, in research around the conservation of PD. However, studies where PD has been specifically included into current spatial conservation practices, namely by incorporating PD into spatial optimisation analyses using tools such as MARXAN, remain rare, although this is changing. There is also a need for further investigation into whether species richness can act as an effective surrogate metric for PD. The dominant approach to incorporate PD into protected area planning, identified in the literature review, is to use phylogenetic tree branches as conservation features, weighted in accordance to their length. This approach, which is referred to here as the “weighted branch-based approach”, was used in a new case study on primates, using MARXAN, to compare the priority areas identified for the conservation of PD with those identified using species-based targets. Large spatial mismatches were found between planning outputs based on PD when compared to outputs based on species, although this was influenced by the availability of area, with the largest mispatches found when area was limited most. No major difference was observed between the amount of PD captured by a PD-based approach versus the amount captured by a species-based approach, suggesting that species richness may be a suitable surrogate metric for PD. Potential issues associated with constraining a planning process in order to account for PD, *e.g.* getting MARXAN to solve a problem (maximum coverage) that is different to one it was designed to solve (minimum set), provided the impetus to seek a new methodology that accounts for PD while still maintaining MARXAN's core functionality. This novel method, which maximises PD though the optimised selection of species that can then act as conservation features to set coverage targets for, was tested using a case study for three mammalian orders (Artiodactyla, Carnivora, and Primates). The results of this case study show that differences in PD between species can be used to select sets of species that maximise overall PD within a spatial conservation planning exercise, without the use of penalties or thresholds that are required in a weighted branch-based approach. Despite heated debate, few studies have tried to empirically investigate the impact of changes in species-level taxonomy due to the use of different species concepts (and specifically the use of the Phylogenetic Species Concept [PSC], which tends to recognise more species than other commonly-used concepts) on the conservation of biodiversity. The final research element of this work specifically addresses this gap in knowledge by presenting the first study to analyse the impact of changes in species-level taxonomy on a PD-informed spatial conservation plan, using African bovid species (gazelles, antelopes etc.) as a case study. PD-informed spatial conservation planning has been argued to be relatively unaffected by changes in species-level taxonomy. However, the results presented here show that, while the amount of area required does not change, there are substantial impacts on the location of spatial conservation plans for African bovid species, depending on whether or not a PSC-based species-level taxonomy is used. Collectively, this thesis shows that PD can be successfully incorporated into conservation planning and that it has a major impact on spatial planning outcomes, particularly when resources (in this case, area) are limited. Based on these findings, there is a clear need for future research to investigate the potential for some metrics, for which data may be more readily available *e.g.* species richness, to act as surrogates for other metrics that capture important dimensions of biodiversity *e.g.* PD; and that in combination with surrogates there is a need for more integrated approaches to conservation that account for the multidimensional characteristics of biodiversity, as well as further investigation into the implications of taxonomy for biodiversity conservation.

CHAPTER 1 INTRODUCTION

Biodiversity is vital for maintaining ecosystems services globally, at all spatial scales (Cardinale et al., 2012; Faith, 1992; Pollock et al., 2017), and so life on Earth, as we know it, is dependent on this biodiversity. However, biodiversity is decreasing globally at an unprecedented rate. An ever-growing human population, with ever increasing levels of consumption, has caused huge declines in biodiversity worldwide (Butchart et al., 2010; Pimm et al., 2014). The scale of this decline is so massive, with species extinction rates between 100-1000 times greater than typical background levels estimated from the fossil record (Ceballos et al., 2017; Pimm and Raven, 2000), and so strongly linked to human actions (Ceballos et al., 2017; Chapin et al., 1997), that biodiversity loss and the prevention of this has long been regarded as a globally important issue (Brooks et al., 2006).

The global importance of conserving biodiversity has been widely recognised within the scientific literature (*e.g.* Brooks et al., 2006; Lamoreux et al., 2006; Sala et al., 2000); this importance is also reflected in international policy. The Convention on Biological Diversity (CBD) is a good example of this: created in 1992-3, the CBD commits its 196 signatory countries to support the global conservation of biological diversity, sustainable use of its facets, and equal sharing of its benefits (https://www.cbd.int/convention/articles: Article 1. Objectives).

Extensive conservation efforts exist, on both global and local scales (Sutherland et al., 2011). However resources are often a limiting factor, and so maximising conservation output with limited resources is a major aim of conservation (Margules and Pressey, 2000). This issue of limited resources is exacerbated by the uneven distribution of biodiversity and its threats, as well as the unequal spread of global wealth (Brooks et al., 2006; Sutherland et al., 2011; Waldron et al., 2013). For example, Waldron et al*.* (2013) found that 40 of the most severely underfunded countries, in regard to money spent of conservation, contained ~32% of all threatened mammalian diversity, and harboured some of the most biodiverse regions in the world.

Spatial conservation planning accounts for this uneven distribution of biodiversity and threats, and is therefore key to conserving biodiversity (Brooks et al., 2006; Margules and Pressey, 2000). Spatial conservation planning can be defined broadly as the design, in regard to shape and location, of conservation areas (Bottrill and Pressey, 2012). In reality however, this process and its results can be extremely nuanced, focusing on managing activities in space that best support the conservation features in question (conservation features being anything that a conservationist may want to protect, for example habitat type or species range). Spatial conservation planning does not always result in a strict protected area where all harmful activities are banned and human access is limited, but may instead restrict and modify anthropogenic activities, with an understanding that socio-economic factors must also be considered (Bottrill and Pressey, 2012; Margules and Pressey, 2000). Spatial conservation planning, specifically the creation of protected areas, is discussed in more detail below in section 1.1.

Evolution is the fundamental underlying process that generates and maintains biodiversity (Beger et al., 2014; Pressey et al., 2003). Given this, and with the main goal of conservation being to protect representative samples of biodiversity and ensure they persist (Cabeza and Moilanen, 2001), it seems self-evident that evolutionary processes and associated metrics should be considered within spatial conservation planning (Faith, 1992). However, to date, examples of evolutionarily-informed approaches to conservation remain rare, with taxonomic metrics such as species richness (which do not fully take into account evolutionary patterns and processes) being traditionally used to inform conservation planning (Beger et al., 2014). While the importance of considering evolutionary processes in biodiversity conservation has been acknowledged in the literature for several decades (Ashley et al., 2003; Crandall et al., 2000; Faith, 1992; Moritz, 2002) it is only relatively recently that it has started to make its way into conservation planning studies and research (Beger et al., 2014; Carvalho et al., 2017; Cowling and Pressey, 2001; Klein et al., 2009; Vasconcelos et al., 2012); with initial studies that analysed the spatial patterns of species richness and evolutionary diversity (the latter of which takes into account evolutionary history) finding spatial mispatches between the two (Forest et al., 2007; Zupan et al., 2014). The lack of explicit evolutionary considerations within spatial conservation planning, coupled with the increasing need to improve the effectiveness of global conservation, is the major motivation for this thesis, with its overarching aim being to advance the field of spatial conservation planning by developing improved approaches for incorporating evolutionary considerations. The main approach to this here is to use existing, state of the art techniques to identify priority areas for the conservation of evolutionary metrics, and to develop novel approaches that more effectively achieve this aim.

As a starting point, it is necessary to clearly and unambiguously define what is meant by "spatial conservation planning" and "evolutionary considerations".

1.1 SPATIAL CONSERVATION PLANNING

Spatial conservation planning is defined as the design of conservation areas (Margules and Pressey, 2000), but in this thesis it will be used more specifically to refer explicitly to protected areas. A protected area is, in its broadest sense, a delimited geographical area that has specific restrictions on human activities to achieve the long-term conservation of biodiversity (Jenkins and Joppa, 2009). The long history and development of protected areas has resulted in their widespread use and their incorporation within one of the CBD's key Aichi 2020 targets, which aimed to have all 196 signatory nations to commit to having at least 17% of terrestrial (including inland water) areas and 10% of marine areas conserved through protected areas by 2020 (Strategic Plan for Biodiversity 2011-2020. Aichi Biodiversity Targets; https://www.cbd.int/sp/targets/).

The preservation and protection of areas of the environment that are deemed to be important is not a new idea in human society; we have protected areas of spiritual or economic importance throughout history (Margules and Pressey, 2000). These areas have been selected on an *ad hoc* basis. As our ecological knowledge has increased over time, the rationale behind designating areas has evolved and shifted towards offsetting biodiversity loss (Spalding et al., 2008). However, despite a similarly improved understanding of evolution, the manner in which areas have been selected and protected does not seem to have changed to the same degree *e.g.* tending to focus on the visually observable patterns of biodiversity *i.e.* species richness and biodiversity hotspots, rather than the processes that generate and maintain this biodiversity (Pressey et al., 2007). This failure to take into account evolutionary processes is likely a result of methodological problems, with such processes being difficult to quantify and incorporate into spatial conservation planning (Faith, 2002). This is coupled with a lack of good, comprehensive data regarding the evolutionary relationships (phylogeny) of organisms, which is key for calculating many evolutionarily-informed metrics that have been proposed for use in conservation (Faith, 1992; Isaac et al., 2007; Mace, 2004; Rosauer et al., 2009; Tucker et al., 2019). However, as evolutionary data has become more available and reliable, there has been an increase in evolutionary considerations within spatial conservation planning studies (Gumbs et al., 2020; Pollock et al., 2015; Strecker et al., 2011).

1.2 EVOLUTIONARY CONSIDERATIONS

As already noted, evolutionary processes generate patterns of biodiversity (Beger et al., 2014). However, these evolutionary processes are complex and multi-faceted; in order to explicitly incorporate them within spatial conservation planning exercises, well-defined, quantifiable, and spatially-based evolutionary metrics need to be identified and used. Descriptors of genetic diversity and evolutionary history are important metrics of evolution and its processes, and they can be mapped across space (Bowen, 1999; Crozier, 1997; Faith, 1992). Genetic diversity is defined here as any measure that quantifies the amount of genetic variability within a population (Hughes et al., 2008). It provides the raw material for evolution by natural selection (Fisher, 1930). The genome of an organism is involved in determining its vulnerability to environmental change, by characterising physiological tolerances, behavioural traits, evolutionary potential for adaptation, and dispersal ability (Beger et al., 2014; de Carvalho et al., 2010). Genetic diversity can provide vital information on a species' long-term persistence and adaptive potential (Stillman, 2003), with metrics such as intraspecific genetic diversity providing this information in a way that can be utilised in spatial prioritisation. The importance of genetic metrics, and the development of methods that allow them to be incorporated into spatial conservation planning, is starting to be reflected more frequently in the literature (Beger et al., 2014; Nielsen et al., 2017). Evolutionary diversity, meanwhile, is often quantified through the metric phylogenetic diversity (PD) (Faith, 1992). PD is calculated by summing the branch lengths joining a species, or set of species, to the root of a phylogeny in which it or they are present (Faith, 1992; Rosauer et al., 2017) (see Figure 1.1). It is important to note that for PD to be calculated accurately, the branch lengths of the phylogeny being used must either be proportional to the amount of evolutionary change (*e.g.* the estimated number of substitutions per site, if using DNA sequence data), or, more commonly, are proportional to time (*e.g.* millions of years), typically the result of a molecular clock analysis. If the branch lengths of the phylogeny being used are proportional to time, then PD represents the amount of unique evolutionary history (in temporal units) a particular branch, species, or clade contributes to the "Tree of Life" (Faith, 1992; Rosauer et al., 2017).

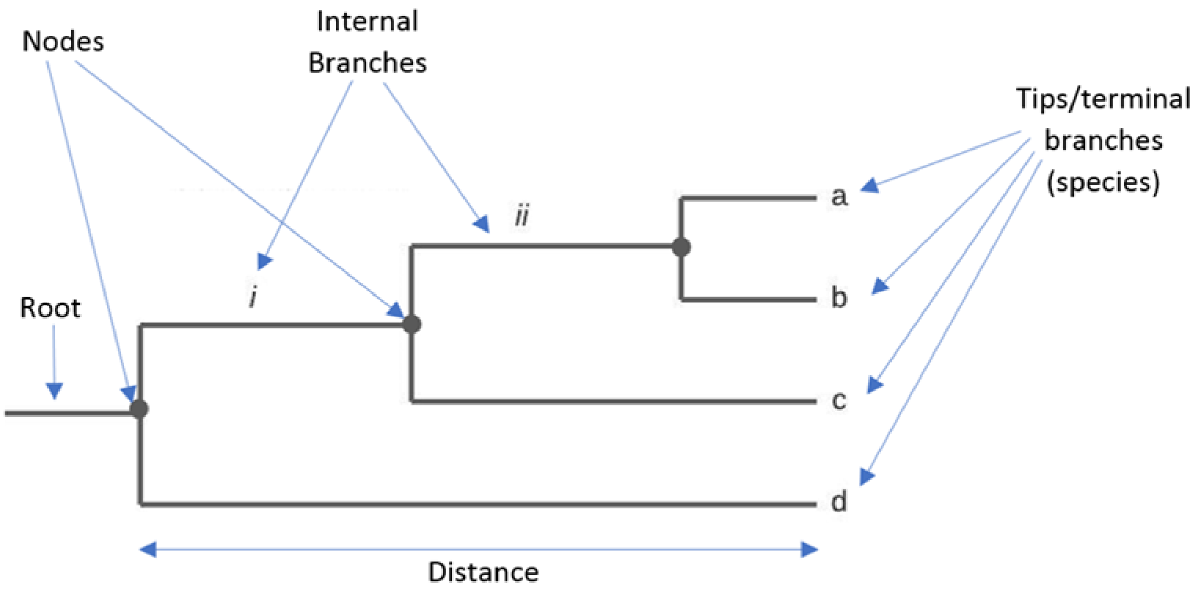

Figure 1.1 Generalised phylogenetic tree, depicting the most important tree elements. Branch length, depicted as distance here, is proportional to the evolutionary divergence between two nodes, or a node and a tip. The length of a branch, on a time-scaled tree (= “chronogram” or “timetree”), as used in this work, is based on temporal divergence (calculated based on estimates of divergence times, usually as the result of a molecular clock analysis) usually in millions of years, or the proportion of the overall time from root to tip.

The inclusion of PD within protected area planning can have important benefits. PD represents a key component of biodiversity, as it reflects evolutionary history, and it may also predict a species’ or clade’s ability to adapt to future conditions (Cadotte et al., 2012; Faith, 1992, 2008; Isaac et al., 2007). In addition, PD may be a proxy for functional diversity (Cadotte and Davies, 2010; Vane-Wright et al., 1991), although this has been disputed in recent years (Devictor et al., 2010; Fritz and Purvis, 2010; Mazel et al., 2018; Zupan et al., 2014). PD also gives planners an insight into evolutionary distinctiveness, which is a measure of how isolated a species is on a phylogenetic tree (Cadotte & Davies, 2010; Isaac et al., 2007; Vane-Wright et al., 1991), as well as potentially helping reduce extinction rates: there is a growing body of evidence that indicates that extinction is not random across the tree of life, but that threatened species that represent greater amounts of PD are more likely to be threatened (Purvis et al., 2000). Furthermore, PD is not distributed evenly across the globe, and spatial mismatches exist between patterns of species richness and PD (Forest et al., 2007; Sechrest et al., 2002). Thus, it is now recognised by multiple authors (Carta et al., 2019; Carvalho et al., 2017; Gumbs et al., 2020; Owen et al., 2019; Pollock et al., 2015; Rosauer et al., 2017, 2018) that spatial prioritization could benefit from the use of PD to inform decision making.

1.3 AIMS AND APPROACH:

The overarching aim of this thesis is to facilitate the integration of evolutionary considerations into spatial conservation planning. Specifically, in this thesis, spatial conservation planning refers to the creation of protected areas, which are a central component to many conservation approaches, traditionally, and moving forward (Margules and Pressey, 2000; CBD, Strategic Plan for Biodiversity 2011-2020, Aichi Biodiversity Targets (https://www.cbd.int/sp/targets/); Visconti et al., 2019); with a specific focus here on spatial conservation using tools that utilise optimisation algorithms (*e.g.* MARXAN and Zonation) as these approaches are widely used by stakeholders.

PD has been chosen as the preferred metric to quantify evolutionary diversity. Only one evolutionary metric has been used, in order to produce a well-defined and coherent thesis that provides detailed insight into a specific aspect of evolutionarily-led conservation. PD was chosen as it captures evolutionary history, it is also a vital part of biodiversity that contributes to ecosystem stability and the adaptability of species and should be considered within future conservation plans to increase their ability to conserve biodiversity (Cadotte and Davies, 2010). This is also reflected within international conservation organisations, as since the time that work on this thesis started (2016) the International Union for Conservation of Nature's (IUCN) Species Survival Commission set up a Phylogenetic Diversity task force specifically with the aim of providing leadership and support for the inclusion of PD in conservation (https://www.iucn.org/commissions/ssc-groups/cross-cutting/phylogenetic-diversity-task-force). PD is also recognised within the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services' (IPBES) 2019 global assessment report as being an indicator of one 'Natures' contribution to people' (https://www.ipbes.net/global-assessment).

Chapter 2 is an extensive review of the peer-reviewed literature, including a structured element, in order to understand and analyse the current state of the art regarding the integration of evolutionary considerations (and particularly PD) into spatial conservation planning. This literature review informs three research chapters, ending with a discussion chapter. The first of these research chapters (Chapter 3) presents a new case study using a state of the art method to identify priority areas for the conservation of primate PD. This case study also included the identification of priority areas for the conservation of primate species richness, which allowed for comparisons to be made with the PD-based approach, as well as an analysis of the potential for species richness to act as a surrogate for PD. As a result of some of the shortcomings identified within the approach used in Chapter 3, the next research chapter (Chapter 4) presents a novel method for the inclusion of PD within a spatial conservation plan that optimises the selection of species to maximise PD without the need to restrict the conservation tool or use penalties to account for PD. Chapter 4 also presents an analysis of how the relationship between the area required to capture different amounts of PD varies between clades (specifically the mammalian orders Artiodactyla, Carnivora, and Primates). The final research chapter (Chapter 5) analyses the impact of taxonomic changes, specifically the use of the Phylogenetic Species Concept (PSC) instead of the Biological Species Concept (BSC), on PD-based spatial conservation planning and more broadly to conservation overall, using African species of the family Bovidae (gazelles, antelope etc.) as a caste study. The question of what exactly species are, and how they should be defined and recognised, continues to be debated within the literature, with current controversy focused on whether or not to use the PSC, which typically results in recognition of a greater number of species than the BSC does. This controversy does not, as yet, show any sign of reaching a consensus, but it is recognised that use of the PSC instead of the BSC may have major impacts to the conservation of species (Christenhusz, 2020; Garnett and Christidis, 2017; Gippoliti, 2019; Gippoliti and Groves, 2013; Zachos, 2015, 2018). Chapter 5 is the first study of its kind to analyse the impact of taxonomic changes on spatial conservation planning and provides important insight to the problem of taxonomic uncertainty, specifically from the perspective of conserving PD, which is an approach that has been argued to be more resilient to taxonomic changes than species richness-based approaches (Faith, 2002) although this has, up until now, never been tested.

CHAPTER 2 THE INCLUSION OF PHYLOGENETIC DIVERSITY WITHIN OPTIMISED SPATIAL CONSERVATION PLANNING –THE STATE OF THE ART

2.1 INTRODUCTION

The importance of including evolutionary information within conservation has long been acknowledged (Ashley et al., 2003; Crandall et al., 2000; Faith, 2002; Moritz, 2002); however, explicit inclusion of evolutionary metrics (for example, phylogenetic or genetic diversity) within spatial prioritisation studies remains rare, with taxonomy-based metrics, such as species richness, being favoured traditionally (Brooks et al., 2006; Brum et al., 2017). This is likely due to a combination of factors, primarily relating to a lack of appropriate phylogenetic data, coupled with a widespread assumption that areas selected based on species ranges will adequately account for evolutionary history (Diniz-Filho and Bini, 2011; Waples et al., 2008). However, there is now empirical evidence, and theoretical arguments, to the contrary (Brum et al., 2017; Devictor et al., 2010; Pollock et al., 2015). Over the last decade, as resource-limited biodiversity conservation has become an ever increasingly important global issue (Ceballos et al., 2015, 2017; Pimm and Raven, 2000; Sandbrook et al., 2019), the field of evolutionary-based spatial conservation planning has, with the help of more complete and more easily accessible data sources, become more widespread and influential (Faith, 2019; Isaac et al., 2007; Tucker et al., 2019). This chapter aims to provide an up-to-date critical review of these studies.

This review begins by discussing the background to PD and its use within spatial conservation planning, before moving on to a structured review of how PD has been incorporated into spatial conservation planning using optimisation tools. The studies selected in the structured review are then broken down and explored, first coarsely to identify major methodological approaches, and then discussed in more detail to highlight the major findings in the field thus far and also to identify where there are gaps in the field and where the field needs further research; this providing the basis for the research chapters that follow.

2.1.1 PHYLOGENETIC DIVERSITY AND SPATIAL CONSERVATION PLANNING

In a seminal 1992 paper entitled ‘Conservation evaluation and phylogenetic diversity’, Daniel Faith stated that conservation biology will falter without addressing the gap between basic conceptual representations of biological diversity and the actual practical working definitions of biological diversity. Faith (1992) went on to state that conservation often has to operate with limited resources, which result in the need to prioritise, and noted that species that are more taxonomically distinct are expected to make larger contributions to the overall measure of diversity; this becomes apparent if species are replaced as the basic units of diversity with features of species. Species that are more taxonomically distinct will contribute more to the diversity of a given subset because they contribute different '*features'*; diversity being important as it gives the "raw material" for change, or the potential to adapt to change, and provides what, some called at the time and still a useful term today 'option value': a safety net of biological diversity, to respond to unpredictable events (McNeely et al., 1990). However, while this is useful, and helps bridge the gap between the basic concepts of biological diversity and the actual practical requirements for successful conservation, these 'features' are not always explicitly enumerated, and a further issue of deciding what features to measure arises (Faith, 1992). Faith (1992) concluded that a measurable indicator of feature diversity was needed, and he introduced the concept of phylogenetic diversity or PD, which he argued is an effective indicator of underlying feature diversity, or the above mentioned 'option value'. Faith's (1992) PD is calculated as the sum of the branch lengths (either proportional to time, or proportional to amount of evolutionary change) of the phylogeny for a particular species or subset of species present in the tree. Faith's (1992) initial reasoning makes the assumption that functional diversity can be captured by PD, but this is now known not always to be the case (Brum et al., 2017; Fritz and Purvis, 2010; Mazel et al., 2018).

Faith (1992) went on to use this PD metric to re-examine protected areas selection scenarios based on a phylogeny of bumblebees, and found 'quite different' priorities when compared to an earlier study that had used taxonomic diversity for this purpose (Vane-Wright et al., 1991). It is important however to note the similarities between Vane-Wright et al.'s (1991) taxonomic distinctiveness and Faith's (1992) PD, as they both were trying to emphasis the same thing, that species were not equal in the amount of diversity they represent. Taxonomic distinctiveness does take into account the branching pattern of a phylogeny *i.e.* the underlying tree structure, but unlike PD it does not include branch lengths (Faith, 1992). Both metrics are therefore different from species richness and also each other, with PD becoming the more widely-used metric within conservation planning.

Despite the impact Faith's work (1992) has had on the conservation biology literature, having been cited over 2,250 times (Web of Science Core Collection 20/10/2020), there has been relatively little explicit use of PD in spatial conservation in the 28 years since it was published (see structured review below in section 2.3). There are likely to be several, interlinked reasons for this, some as the result of a lack of understanding and a poor discourse between key factions in the world of biodiversity conservation, but the main driving force is likely to be high impact studies that conclude that species richness is a good surrogate for PD. In one such study Brooks et al. (2006) made the conclusion from their review of published concepts and methods behind global conservation prioritisations, that even if PD is not explicitly targeted, prioritisations based on species richness provide a solid surrogate for evolutionary history. However, given the potential efficacy and practicality of PD, and the importance of evolution to biodiversity, it would be unwise to assume that PD is fully concordant with species richness in all clades. This was the viewpoint of Forest et al. whose 2007 publication neatly demonstrated that species richness and PD are decoupled in the flora of a biodiversity hotspot, the Cape of South Africa. They used a biome-wide phylogenetic analysis of 735 of the 943 genera of angiosperms recognised in the region and compared it to species and genus richness for the same region on the same spatial scale. While there were, as expected, similar spatial patterns between species richness and PD, with the result initially indicating that species and genus richness appear to be good proxies for PD in conservation planning for the region, the similarities were hiding key differences. While PD seemed to scale with species and genus richness, this scaling was complex, with some regions having more or less PD than would be expected based on their species and genus richness. These results indicate that the sole use of species and genus richness in spatial conservation planning may not adequately capture PD and underline the importance of including PD as a distinct metric. The uptake of PD within conservation more broadly, stemming from Faith's (1992, 1996, 2002, 2019) pioneering work, is presented in Figure 2.1. There is clear evidence of consistently increasing research interest in PD and conservation (Figure 2.1). To further quantify and analyse this trend, a structured review of publications that discuss both PD and conservation, following the general approach of Okoli (2015), was undertaken.

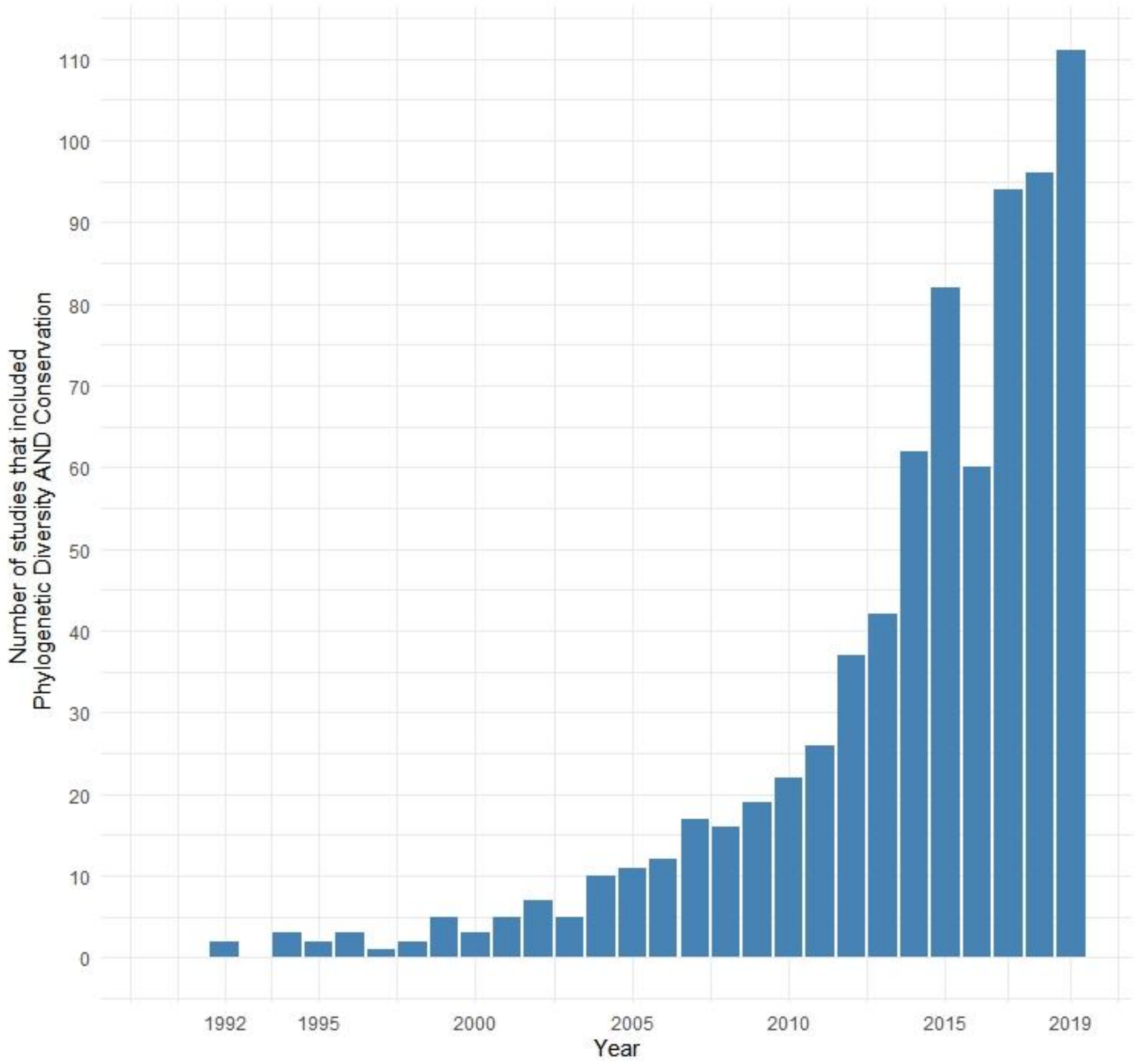

Figure 2.1 The number of studies published each year that have included "Phylogenetic Diversity" AND "Conservation" within their title and/or abstract. Identified within Web of Science's core collection, from 1900-2019, 0 studies identified before 1992, 89 studies published in 2020 as of date of search (20/10/2020)

2.2 METHOD

The parameters of the structured review are as follows: Peer reviewed papers that have explicitly included PD into a spatial conservation planning exercise using an optimisation tool, such as MARXAN or Zonation. Case studies were chosen specifically as the main aim of the search was to identify approaches used and their development up to the present.

The review was conducted using the Web of Science's (WoS) core collection, using the widest available date range (1900-2020). Personal specialist knowledge of the topic was used to initially to select keywords. Table 2.1 shows the final list of keywords used with WoS, identifying papers that had included any of these within their title or abstract. Abstracts were read from all identified papers, with those indicating the incorporation of PD into a spatial planning exercise read in full to confirm their suitability, or not, for the review. The reference lists of the papers selected for review were also examined to identify any other potentially relevant studies. Any additional keywords that were identified within papers found in reference lists were added and the process was repeated iteratively until all peer reviewed studies in which PD had been explicitly incorporated into a spatial conservation plan using an optimisation tool had been identified. The selected papers were read in full to evaluate the premise, methods, and conclusions of each study.

Table 2.1 The key words used iteratively in the structured review. Used to identify all studies where phylogenetic diversity has been explicitly integrated into a protected area planning exercise, including number of total studies each search returned (figures presented from 20/10/2020). Boolean operators used: AND (all search terms must occur to be retrieved), " " (retrieves documents that contain the full term or phrase. Truncations used: * zero or more characters

Key words used	**Number of studies identified**
"phylogenetic diversity" AND conservation	n = 845
***phylogen* AND "spatial conservation"**	n=13
***phylogen* AND "spatial *priori*"**	n = 5
***phylogen* AND Marxan**	n = 4
***phylogen* AND Zonation**	n = 166
***phylogen* AND "conservation prior*"**	n=436
***phylogen* AND "protected area*"**	n = 326
***phylogen* AND "conservation plan*"**	n = 315
Total	n = 2110

2.3 RESULTS

The structured review identified 13 studies that incorporated phylogenetic diversity into a spatial conservation planning exercise using an optimisation tool to identify priority areas for the conservation of evolutionary history. The key findings from these studies are presented in Table 2.2. The first study identified was in 2002 (Rodrigues and Gaston, 2002), with the next studies not being published until 2014 (Asmyhr et al., 2014; Sobral et al., 2014) marking the start of regular publication of studies, with the most recent being from 2019 (Carta et al., 2019; Rapacciuolo et al., 2019; Sibarani et al., 2019). It is worth noting here that Strecker et al. (2011) was originally included, as their work supposed to define conservation priorities for freshwater fishes according to phylogenetic diversity, as well as taxonomic and functional diversity. However, upon further inspection, due to a lack of availability of a robust phylogeny for their study species (desert freshwater fishes) they did not include branch lengths, meaning it was not a true incorporation of PD, as described by Faith (1992) but closer to Vane-Wright et al.'s (1991) taxonomic diversity (see section 2.1.1). This work was therefore excluded from the review as it would be difficult to draw conclusions from their work that would be useful for this review.

The dominant (7 out of 13 studies, *i.e.* ~54%) approach used to incorporate PD is a weighted branch-based approach, where the individual branches of the phylogeny are treated as individual conservation features, and with PD accounted for by assigning a weighting to each branch proportional to its length; the higher the weighting, the more important the conservation feature, in this case the branch, to the conservation plan. The first study to do this was Asmyhr et al. (2014), looking at the conservation of groundwater ecosystems.

The next most popular approach was phylogenetic eigenvectors (two studies); initially used by Brum et al. (2017) who synthesised information on PD in eigenvectors by conducting a principal coordinate analysis (PCoA) based on phylogenetic distances between species. They then generated multiple eigenvector scores for each species that represented the relatedness of each species to each other species at different phylogenetic levels. Of the 4,546 genetic axes from the PCoA, Brum et al. (2017) selected 16 eigenvectors, as these represented 63% of the total variation in the distance matrix, and the addition of more eigenvectors did not provide any more significant information. For each eigenvector, species were split into 20 equal-sized phylogenetic groups, in which the species were grouped based on their phylogenetic affinity in a given phylogenetic level. Brum et al. (2017) then multiplied the binary species X phylogenetic group matrix by a grid cells X species matrix which resulted in a site X phylogenetic group matrix, where the number of each species belonging to a particular phylogenetic group was known for each section of their planning area. This gave them the spatial range for each phylogenetic group and allowed for the utilisation of Zonation to maximise PD in a protected area. This approach of using phylogenetic eigenvectors was later also used by Sibarani et al. (2019). The other approaches to incorporating PD - mean pairwise distance, Rao’s quadratic entropy (Rao, 1982), and a combined branch lengths for each cell (hotspot) approach were used only once.

Of the 13 studies, 12 used either Zonation, MARXAN, or both for optimisation: Zonation was used by eight studies and MARXAN was used by five (one study used both). C-PLEX and Prioritizr were the other tools used; C-PLEX (ILOG, 1999) is the only optimisation tool that is not specialised for spatial conservation, it can solve the ‘minimum set problem’ akin to MARXAN and the ‘maximum coverage problem’ akin to Zonation. Prioritizr is the newest tool, identified here, for spatial conservation planning and reports that its finds ‘much cheaper’ solutions than MARXAN, and more quickly (https://prioritizr.net/).

The studies showed a broad range in scale, both spatially and taxonomically. However, the more recent studies showed a trend towards large areas and large clades, with nine studies being at least at the national scale, with three of these being global studies averaging in excess of 1000 species, with terrestrial mammals being the favoured group (six studies);

however, one study included all terrestrial tetrapods across the Americas (10,213 species) (Rapacciuolo et al., 2019).

Table 2.2. A breakdown of the studies identified by the structured review, highlighting key information on methodologies and findings.

Title	*Citation*	*Method of PD incorporation*	*Spatial optimisation tool used*	*Scale*		*Amount of overlap with a species richness approach*	*Other metrics of biodiversity explored*	*Evidence for surrogacy between metrics*
				Spatial	*Taxonomic*			
Maximising phylogenetic diversity in the selection of networks of conservation areas	Rodrigues and Gaston (2002)	Maximum PD with full representation of every branch	**C-Plex** (Solving the 'Minimum Set Problem' and the 'Maximum Coverage Problem')	Regional (north west South Africa)	Birds (166 species)	Distinct differences in location of sites	No	No
Structured Conservation Planning for Groundwater Ecosystems Using Phylogenetic Diversity	Asmyhr et al. (2014)	Weighted branch-based approach	**MARXAN** (Solving the 'Minimum Set Problem')	Regional (New South Wales, Australia)	Stygofauna (distinct invertebrate fauna) (n= unknown)	N/A	No	N/A
Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity	Sobral et al., (2014)	Mean Pairwise Distance	**Zonation** (Solving the 'Maximum Coverage Problem')	National (Brazil)	Terrestrial mammals (515 species) and Birds (1581 species)	Distinct differences in location of sites	Functional diversity	N/A

Title	*Citation*	*Method of PD incorporation*	*Spatial optimisation tool used*	*Scale*		*Amount of overlap with a species richness approach*	*Other metrics of biodiversity explored*	*Evidence for surrogacy between metrics*
				Spatial	*Taxonomic*			
Phylogenetic diversity meets conservation policy: small areas are key to preserving eucalypt lineages	Pollock et al. (2015)	Weighted branch-based approach	**Zonation** (Solving the 'Maximum Coverage Problem')	Regional (Victoria, Australia)	Terrestrial plants (96 species)	N/A	No	N/A
Representing Hotspots of Evolutionary History in Structured Conservation Planning for European Mammals	Arponen and Zupan (2016)	Rao's quadratic entropy (Rao, 1982)	**Zonation** (Solving the 'Maximum Coverage Problem')	International (Europe)	Terrestrial mammals (275 species)	Distinct differences in location of sites	No	N/A
Global priorities for conservation across multiple dimensions of mammalian diversity	Brum et al. (2017)	Phylogenetic eigenvectors	**Zonation** (Solving the 'Maximum Coverage Problem')	Global	Terrestrial mammals (4547 species)	Distinct differences in location of sites	Functional diversity	N/A
Spatial conservation prioritization of biodiversity spanning the evolutionary continuum	Carvalho et al. (2017)	Maximising unique combined branch lengths for each cell	**Zonation and MARXAN**	International (Iberian Peninsula)	Amphibians (27 species) and Reptiles (50 species)	Distinct differences in location of sites	Intraspecific lineage diversity	In the absence of phylogenetic data, the use of species ranges seems to be a suitable surrogate

Title	*Citation*	*Method of PD incorporation*	*Spatial optimisation tool used*	*Scale*		*Amount of overlap with a species richness approach*	*Other metrics of biodiversity explored*	*Evidence for surrogacy between metrics*
				Spatial	*Taxonomic*			
Large conservation gains possible for global biodiversity facets	Pollock et al. (2017)	Weighted branch-based approach	**Zonation** (Solving the 'Maximum Coverage Problem')	Global	Terrestrial mammals (4787 species) and Birds (9993 species)	Distinct differences in location of sites	Functional diversity	N/A
Phylogenetically informed spatial planning is required to conserve the mammalian tree of life	Rosauer et al. (2017)	Weighted branch-based approach	**MARXAN** (Solving the 'Minimum Set Problem') and **Prioritizr**	Global	Terrestrial mammals (4778 species)	Distinct differences in location of sites	No	Yes – better surrogacy when area was less restricted, however poor surrogacy under increased area restrictions
Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy	Rosauer et al. (2018)	Weighted branch-based approach	**MARXAN** (Solving the 'Minimum Set Problem')	Regional (Kimberley, Australia)	Skink and gecko lizards (46 species)	N/A	No	N/A

Title	***Citation***	***Method of PD incorporation***	***Spatial optimisation tool used***	***Scale***		***Amount of overlap with a species richness approach***	***Other metrics of biodiversity explored***	***Evidence for surrogacy between metrics***
				Spatial	***Taxonomic***			
Phylogenetically informed spatial planning as a tool to prioritise areas for threatened plant conservation within a Mediterranean biodiversity hotspot	Carta et al. (2019)	Weighted branch-based approach	**MARXAN** (Solving the 'Minimum Set Problem')	National (Italy)	Terrestrial Plants (995 species)	N/A	Evolutionarily Distinct and Globally Endangered (EDGE) metric (Isaac et al., 2007)	N/A
Species richness as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas	Rapacciuolo et al. (2019)	Weighted branch-based approach	**Zonation** (Solving the 'Maximum Coverage Problem')	International (Across the Americas)	Tetrapod vertebrates (10,213 species)	Distinct differences in location of sites	Functional diversity	Yes - species richness represents phylogenetic and functional diversity well
Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island	Sibarani et al. (2019)	Phylogenetic eigenvectors	**Zonation** (Solving the 'Maximum Coverage Problem')	National (Sumatra)	Mammals (193 species, including 4 surrogate species)	Distinct differences in location of sites	Functional diversity	No

Nine studies compared a PD approach with a more traditional species richness-led approach; of these nine, all found spatial mismatches between the priority areas identified based on PD versus those based on species. The amount of spatial mismatch varied within and between the studies, but all cited differences between the outputs from the two approaches. Of these nine, despite some assertions of surrogacy in their results based on spatial mispatches, only four presented actual evidence for the potential of surrogacy between metrics *i.e.* one metric being captured within a plan designed to captured another, specifically here of species richness acting as a surrogate for PD. In their work on amphibians and reptiles in the Iberian Peninsula, Carvalho et al. (2017), found that the use of species range data was a suitable surrogate for PD, but major portions of PD would still likely not be protected. Rosauer et al. (2017) showed that the amount of area available played an important part in the amount of PD captured within a species-based approach, with poor surrogacy found when the amount of area available for protection was most restricted. Rapacciuolo et al. (2019) is the only study identified by the parameters of the structured review that explicitly explored the potential for species richness to act as a surrogate for PD. Specifically, Rapacciuolo et al. (2019) found that, for tetrapod species (n= 10,213) across the Americas, priority areas for the conservation of species richness captured PD well. Sibarani et al. (2019) also looked at surrogacy but this was associated with the potential for one particular species to act as a surrogate for important metrics, including PD, for a whole area containing multiple species. Their work was more concerned with how well a conservation plan based around a 'flagship' species, in this case one of four charismatic megafauna in Sumatra (the Sumatran tiger - *Panthera tigris sondaica*, Sumatran elephant - *Elephas maximus sumatranus*, Sumatran orangutan - *Pongo abelii*, and the Sumatran rhinoceros - *Dicerorhinus sumatrensis*), could capture the species richness, PD, and functional diversity of the other species on the Island. Sibarani et al. (2019) found relative low levels of surrogacy but again their work focussed on the ability for priority areas based on one species to capture important metrics rather than one metric being a surrogate for another.

2.4 DISCUSSION

This structured review shows that PD has been incorporated into optimised spatial conservation plans to identify priority areas for the conservation of evolutionary history in 13 published studies to date, with the rate of publication of these appearing to be on the increase: the first study was published in 2002, but 8 studies (= ~62% of the total) have been published between 2017-2019 (also see Figure 2.1). Collectively, these studies have looked at a wide range of taxonomic groups and study areas. While the number of published studies is relatively small, meaning that there is a limitation to the strength of the conclusions that can be drawn, these studies do capture some important findings, including the spatial mismatch between priority areas for the conservation of PD and species richness. The studies identified also highlight the need for further research, not only in the sense that additional case studies are needed to strengthen existing conclusions, but also more specifically that there is a lack of work on the potential for metrics to act as surrogates for each other, and practically no work on the impact of taxonomic changes to the spatial conservation of species, something that has been discussed as a potential issue within the taxonomic literature (Garnett and Christidis, 2017; Gippoliti and Groves, 2013; Zachos, 2015).

2.4.1 INCORPORATING PD

When Faith (1992) presented PD as an element of biodiversity separate from species richness, not only did he propose that PD could act as a “safety net” to ensure that biological diversity can respond to changing conditions, but he also proposed a formal method for quantifying PD, namely by calculating it as the sum of branch lengths. Species themselves, without the use of phylogeny, cannot provide accurate information on the amount of PD they capture (Faith, 1992, 2002). Furthermore, the amount of PD a species does capture within a planning area is dependent on which other species are contained within that planning area, and how closely related those species are. For example, if the selection of a planning area adds a species that is closely related to another species that is already within the planning area, and this additional species has also only relatively recently diverged, not only will internal branches of the phylogeny leading to this additional species already be included within the conservation plan, due to the presence of the original species, but the terminal branch added does not represent much additional PD. Compare this example to a situation where the addition of a planning area captures a species that is distantly related and where many of the internal branches are not already included within the existing protected area, the amount of additional PD now included in the protected area far outweighs the first example, although the amount of area and number of species is exactly the same. Decomposing a phylogeny into its constituent features, *i.e.* its branches, allows planners to identify priority areas for the conservation of PD across space by maximising complementarity in the distribution of internal branches via optimisation algorithms now common in modern spatial planning, for example by Rosauer et al., (2017, 2018). In its most basic form, a weighted branch-based approach views each branch in a phylogeny as a separate conservation feature with its own range, which is calculated as the union of the ranges of the tips (= species in a species-level phylogeny) that descend from it (Rosauer et al., 2017). PD can then be explicitly accounted for through branch lengths via applying a weighting that is proportional to branch length, added in the optimisation algorithm (*e.g.* Pollock et al., 2015; Rosauer et al., 2017; Carta et al., 2019). Other approaches have been used that incorporate PD via phylogenetic distance between species either using mean pairwise distance (Sobral et al., 2014) or phylogenetic eigenvectors (Brum et al., 2017; Sibarani et al., 2019).

A popular way of mapping PD across space is to simply calculate the combined branch lengths within a planning area (counting each branch's occurrence only once) (*e.g.* Forest et al., 2007; Fritz and Purvis, 2010) often using the *Picante* package in R (https://cran.r-project.org/web/packages/picante/picante.pdf). However, this only provides information on PD hotspots and does not provide planners with the full picture of the spatial representation of a phylogeny, meaning substantial portions of evolutionary history may not be included within a protected area; this reflects the wider issue of hotspot versus complementarity approaches in spatial conservation (Shrestha & Wang, 2018). Hotspot approaches, which assign high levels of importance to areas that contain a high level of richness for a particular conservation feature *e.g.* species, have been a popular method in conservation, due to their simplicity to develop, implement, and describe (Ribeiro et al., 2017). However, hotspot methods can be insufficient as areas of richness do not always overlap with areas of rarity or range-restricted conservation features, *e.g.* species, and also therefore phylogenetic branches. If these approaches were to acknowledge this lack of overlap and include important areas outside the hotspots, as well as the hotspots themselves, into a conservation plan, the cost of the plan is likely to increase.

The solution to this problem is to use approaches that do not explicitly look for hotspots but instead use iterative algorithms to optimise the selection of conservation features, in regard to reducing cost *e.g.* area, by utilising the complementarity in the ranges of features (Fox and Beckley, 2005; Pressey et al., 1997; Shrestha and Wang, 2018). An example of this is presented by Shrestha and Wang (2018) in their work on the spatial conservation of 556 Chinese *Rhododendron* species in the mountain forests of China, where a complementarity approach selected less area to capture the equivalent number of species within a conservation plan when compared to a hotspot approach, and actually had higher levels of representation within the complementarity-based plan. The drawbacks of a hotspot approach have likely resulted in it only appearing in one study identified within the structured review here, and even within this study it was presented alongside more comprehensive approaches that accounted for the full representation of PD (Carvalho et al., 2017).

Building on Faith's (1992) initial work on PD, Polasky et al. (2001) were the first to adopt a weighted branch-based approach to identifying priority areas for the conservation of PD in a real-world case-study (531 North American birds). Based on their results, Polasky et al. (2001) identified priority areas for the conservation of PD; however, they did not adopt an optimisation approach, citing computational difficulties, and as such this study has been omitted from the structured review here. Nevertheless, the work by Polasky et al. (2001) informed the first study that did meet the parameters of this review, namely by Rodrigues and Gaston (2002), which in turn formed the basis for the studies that followed. The temporal distribution of the studies highlighted here, including the marked increase after 2011, is broadly reflected in the overall number of studies published that have examined PD and conservation (Figure 2.1). This is likely related to the availability of data, with some of the first comprehensive species-level phylogenies of even a well-studied group like mammals not becoming available until 2007 (Bininda-Emonds et al., 2007), and to the increased importance placed on protecting evolutionary history in recent years (Cadotte et al., 2012; Faith, 2019; Gumbs et al., 2020; Isaac et al., 2007). The importance of PD is further reflected in the recent creation of the Phylogenetic Task Force set up by the IUCN's Species Survival Commission (https://www.iucn.org/commissions/ssc-groups/cross-cutting/phylogenetic-diversity-task-force).

2.4.2 SPATIAL OPTIMISATION TOOLS

Zonation and MARXAN are the most commonly used optimisation tools to identify priority areas for the conservation of PD (Zonation used in eight studies and MARXAN in five), reflecting their widespread use within the field of spatial conservation planning in general. C-PLEX and Prioritizr were only used once. C-PLEX was likely made redundant when more tools, specifically designed for spatial planning, like Zonation and MARXAN, were developed. Prioritizr on the other hand, was likely only incorporated within one study as it is a relatively new tool, one that supposes find much cheaper solutions than MARXAN, and in a much shorter amount of time, it also has the ability to read input data formatted for MARXAN; further work is needed to test the functionality of Prioritizr in the field of PD-informed spatial conservation planning.

MARXAN is the most widely used software for the creation of protected areas in the world (Ball et al., 2009; Watts et al., 2017) and Zonation is also one of the most widely used (Delavenne et al., 2012), being utilised to identify international conservation zones, including parts of the Natura 2000 network across the EU (Simeonova et al., 2017). While both of these tools are designed to optimise protected area selection, the way the tools approach this shared goal is fundamentally different (Alagador and Cerdeira, 2020; Delavenne et al., 2012). MARXAN solves the 'minimum set problem' where the goal is to achieve a minimum coverage target for all conservation features, *e.g.* species ranges, for the smallest possible cost, *e.g.* amount of area; it does this by identifying areas that can meet a set of quantitative, user-defined coverage targets for selected conservation features, while minimising an overall objective function score that can account for various costs (Ball and Possingham, 2000). Zonation, on the other hand, solves the 'maximum coverage problem', which maximises conservation benefits for a pre-defined user specified cost; it does this by calculating the marginal loss of not including each planning unit, calculated iteratively, removing each unit while maximising the conservation value of the units that remain, resulting in a hierarchal ranking of the planning units in the selected area (Moilanen, 2007; Moilanen et al., 2005). Zonation also allows the user to positively weight biodiversity input features for selection, and to negatively weight features that should be avoided, such as threats or pressures (Allnutt et al., 2012).

Both Zonation and MARXAN have been widely used across the globe and the literature. When compared directly, both have been shown to perform similarly, identifying similar priority areas (Allnutt et al., 2012; Delavenne et al., 2012). There are, however, important considerations to make when deciding on which tool to use, these are associated with how their core algorithms operate and the outputs they provide. MARXAN has a stochastic approach that identifies multiple outputs that meet the coverage targets through spatially explicit annealing, with 200 runs per solution being standard practice (Ball and Possingham, 2000). This allows for more flexibility and choice in the outputs for the planner or stakeholder, which may explain why MARXAN is more widely used in spatial conservation planning in general. Zonation on the other hand is deterministic and as such provides a single solution per input. Deterministic outputs make Zonation a more attractive tool to use when investigating differences in the areas selected using different metrics of biological diversity, such as PD versus species richness, which is likely a reason why Zonation is the favoured tool in the studies identified in the structured review.

2.4.3 SCALE

Scale, both in terms of spatial range and in the size of the taxonomic groups being considered, varied greatly within the studies identified here; however, there is a trend through time towards larger areas and clades, particularly higher level clades, that is more apparent in the more recent studies. This range and general skew towards large datasets is likely due to the relatively understudied nature of this field, where investigations are focussed on trying increase the power and applicability of these studies. However, more studies are needed that apply these methodologies on a finer scale to determine applicability and transferability across scales. That is not to say that there are no studies that have explored PD-based conservation using more regional case studies. For example, Rosauer et al. (2018) present a PD conservation strategy in collaboration with local stakeholders and local government for the Kimberly region of north west Australia. Rosauer et al. (2018) provided evidence, beyond conceptual importance and ability, of PD-driven conservation in a successful real-world regional example; identifying priority areas within already managed locations, while also identifying previously under-surveyed regions that contain deeply divergent lineages.

2.4.4 SPATIAL PATTERNS OF PD VS PRIORITY AREAS FOR CONSERVATION

During the process of conducting the structured review, numerous studies were identified that explored spatial patterns of PD and sought to locate hotspots of PD for various clades across different areas (*e.g.* Gumbs et al., 2020; Mazel et al., 2015; Rosauer et al., 2016; Thuiller et al., 2015; Zupan et al., 2014). These studies were not included within the structured review as they did not use an optimisation tool to identify priority areas for conservation, but only identified hotspots, which (as previously discussed in section 2.4.1) is a suboptimal conservation approach (Shrestha and Wang, 2018). However, these studies still provide valuable information for planners, and also act as useful methodological case-studies for the mapping of PD across space, which is a core element for spatial optimisation. Many of these hotspot studies also compared the spatial patterns of PD with that of species richness, and found substantial levels of spatial mismatch between the two (*e.g.* Carta et al., 2018; Lindegren et al., 2018; Wong et al., 2018; Zupan et al., 2014). Spatial mismatches between areas of PD and species richness highlights the importance of conservation strategies that explicitly account for PD. However, they do not act as evidence for spatial mismatches in the priority areas for the conservation of PD versus species richness; this is due to the fact that that range-restricted and rare portions of a phylogenetic tree may not be associated with areas of high species richness, and so once again the issue of hotspots becomes apparent.

2.4.5 SPATIAL MISMATCHES BETWEEN PRIORITY AREAS FOR PD AND SPECIES RICHNESS

The studies included within the structured review that compared results from PD-based optimisations with results from species richness-led optimisations all reported substantial mismatches in priority areas. This provides robust evidence for the spatial incongruence of priority areas that maximise the conservation of PD compared to those that maximise the conservation of species richness. For example, Sobral et al. (2014) used Zonation to compare the spatial conservation priorities identified for the species richness and PD of terrestrial mammals and birds in Brazil. Sobral et al. (2014) found that priority sites for maximising species richness and those that maximise phylogenetic diversity differed significantly, with low congruence between sites. Similar results were found for all the studies that investigated such differences, spanning the full spectrum of spatial scales and taxonomic groups considered by the studies in the review (Table 2.2). These findings add important information to the knowledge base of biodiversity conservation, mainly highlighting the core principle within PD-driven conservation, namely that “all species are not equal”. Although PD is inherently associated with species richness, with more species equating in more PD, not all species are equal in the amount of evolutionary history they represent, and therefore approaches that are based on species richness may not maximise the amount of PD conserved.

Nevertheless, of the studies included, one did conclude that the amount of spatial overlap between priority areas for species richness and PD provide evidence that, under limited data situations, species richness may actually be an acceptable surrogate for capturing PD (Carvalho et al., 2017). However, others found low levels of overlap in priority areas, indicating that these different dimensions of diversity, PD and species richness, often do not act as adequate surrogates for each other (Brum et al., 2017; Sobral et al., 2014). While either of these conclusions, namely that species richness is or is not a suitable surrogate for

PD, may in fact be true, spatial congruence between priority areas is not by itself evidence for or against surrogacy (Rapacciuolo et al., 2019; Rodrigues and Gaston, 2002). This is because, with surrogacy, using overlap between priority areas still results in the same issues associated with hotspots: They do not tell the full story - The areas that are not overlapping, in these spatial mismatches, may represent areas of high, or low, PD, or areas that contain the range of parts of the phylogenetic tree that have or have not been adequately captured within the priority areas for species richness. While not aiming to incorporate a particular metric, a priority area may still include a significant proportion of one metric, particularly if the secondary metric is inherently connected with the other, as species richness and PD are.

2.4.6 SURROGACY

Studies identified within the literature have asserted that spatial mismatches in patterns of PD and species richness mean that species richness cannot act as a surrogate for PD (Devictor et al., 2010; Pardo et al., 2017; Wong et al., 2018; Zupan et al., 2014). This has been reinforced by studies identified in this review that have incorporated species richness and PD into optimised spatial planning approaches and still found mismatches between the two metrics that they also interpret as evidence of poor surrogacy potential (Brum et al., 2017; Sobral et al., 2014). However, as explained by Rapacciuolo et al., 2019, which is the only study identified within this review that explicitly investigates surrogacy potential between metrics: surrogacy is measured in the amount of one metric that is captured within a prioritisation for another, not by spatial congruence between priority areas.

Aside from the studies that assumed species richness to be an acceptable surrogate under situations where data on PD was limited (Carvalho et al., 2017) there are two, including Rapacciuolo et al. (2019) that show evidence for actual surrogacy, the other being Rosauer et al. (2017). Rosauer et al. (2017) explored the efficacy of PD-informed spatial conservation compared to species-based plans for global mammal species, and reported that species-based planning was very poor at capturing PD. However, the performance of species as a surrogate for PD was influenced by the amount of constraint that was placed on the optimisation tool, in this case MARXAN, in the form of available area. Species performed most poorly at capturing PD when compared to the PD approach when the amount of available area was most limited (up to a maximum of 2% global land area). However, the disparity in the amount of PD captured decreased as the amount of available area increased, closing from ~12% to within 2-3% for the examples with the least amount of spatial restriction (Rosauer et al., 2017). This work by Rosauer et al. (2017) indicates that species richness does in fact have the potential to act as a surrogate for PD, but that this is strongly mediated by the amount of land available. It also shows the impact that other factors of an optimisation, *e.g.* cost thresholds, can have on the outputs of a conservation plan. For example, in Rosauer et al. (2017) a decrease in the amount of available land was associated with a decrease in the amount of PD captured within a species-based plan; this may also result in differences between conclusions drawn between studies where the impact of area restrictions are not accounted for, or only one level of available area was used in the analysis.

The work by Rapacciuolo et al. (2019) is the only study identified with the structured review that explicitly sets out to investigate the surrogacy potential of metrics, and is therefore the only study in the literature that does so using an optimisation approach. Rapacciuolo et al. (2019) used Zonation to identify priority areas for the conservation of species richness and PD for terrestrial vertebrates across the Americas, as well as the amount of each metric that is captured by the plans created for the other *i.e.* surrogacy. Rapacciuolo et al. (2019) found that, despite spatial mismatches in the priority areas, a high level of surrogacy was found between species richness and PD (Rapacciuolo et al., 2019). The results from Rapacciuolo et al. (2019) show that it may not always be necessary to include PD data into the spatial conservation process to capture evolutionary history.

2.4.7 UNDERREPRESENTATION OF PD WITHIN EXISTING PROTECTED AREAS

Many studies that have investigated the spatial patterns of PD have shown that current protected areas perform poorly at protecting PD (Daru et al., 2019; Lindegren et al., 2018; Zupan et al., 2014). However, several studies identified in this review have shown through the use of an optimisation approach that, while there is poor representation of PD in current protected area networks, small increases and shifts in protected areas can result in disproportionately large increases in the amount of PD protected (Carta et al., 2019; Pollock et al., 2017; Rosauer et al., 2017). For example, Pollock et al. (2017) show in a global mammal and bird case study that an additional areas increase of 5% can more than triple the amount of PD captured by protected areas, providing further evidence for the power and importance of optimisation approaches to the conservation of biodiversity.

2.4.8 FUNCTIONAL DIVERSITY

Functional diversity is often referred to alongside PD as another aspect of biodiversity that is crucial to protect (Brum et al., 2017). As with PD, functional diversity is distinct from species richness; broadly speaking, it involves understanding ecosystems in terms of what species "do" (the ecological roles they play), rather than their evolutionary history or species-level taxonomy (Petchey and Gaston, 2006). Understanding the functional diversity of an area allows conservationists to generalise the functional contributions of species, and to consider the ecological impact of species going extinct or a change in the species composition of an area (Pimiento et al., 2020).

There is an increasing inclusion of functional diversity into optimised spatial conservation plans, which is reflected in the studies identified by this review. All five studies that included functional diversity found poor overlap between the priority areas for PD, functional diversity, and species richness. Pollock et al. (2017) reported that priority areas for species richness and PD showed a greater degree of overlap with each other than they did with priority areas determined based on functional diversity. However, Brum et al. (2017) showed that PD and functional diversity had considerably more overlap with each other than each had with species richness. Both studies used datasets for global mammal species, with Pollock et al. (2017) including birds as well, and it is unclear the impact the addition of birds had, and it is reasonable to assume they would have had some impact.

2.5 CONCLUSION

"Traditional" approaches to spatial conservation have focussed on maximising species richness (Brooks et al., 2006). However, methodologies that focus exclusively on species may not present the best approach to the conservation of biodiversity, as they do not account for evolutionary history which is associated with ecosystem stability as well as providing the 'option value' that is associated with the ability for the persistence of species in an increasingly fast changing world (Cadotte et al., 2012; Faith, 1992, 2019; Vane-Wright et al., 1991). The majority of species are the result of millions of years of evolution, and if we only focus on the diversity of the species themselves without acknowledging their evolutionary history we may miss out on important and unique ecological and evolutionary information, potential, and resilience (Faith, 1992). PD represents a metric that captures this information, and optimised spatial conservation approaches offer an established and efficient way of protecting it. Robust species-level phylogenies are becoming more widely available for many clades, particularly vertebrates (*e.g.* Bininda-Emonds et al. 2007; Prum et al. 2015; dos Reis et al. 2018; Upham et al. 2019), facilitating the increasing use of PD and other evolutionarily-informed metrics in spatial conservation planning. This review represents not only the most up-to-date synthesis of the state of the art for the incorporation of PD via optimised spatial conservation approaches but in fact the only review of this nature. This review provides a useful tool by documenting and discussing the current methodological approaches to the incorporation of PD within spatial conservation planning, including the benefits and pitfalls of different approaches. This comes at a pivotal time as the field is rapidly increasing. It also provides the base and the jumping off point for the research chapters that are to follow in this thesis, that aim to address some of the key issues identified within the review.

This review shows that since the introduction of PD into the field of conservation by Faith in 1992, only a limited number of studies have included PD into an optimised spatial conservation exercise. Based on the evidence at hand, it seems that this lack in initial uptake was likely due to a lack of available data alongside few recognised methodologies and lack of software for implementing these. As necessary data has become more available, different approaches to the inclusion of PD into spatial conservation have been presented, with what is referred to here as the 'weighted branch-based' approach proving the most popular, and with Zonation being the tool used most frequently. However, the general lack of case studies makes it difficult to draw specific conclusions, particularly on finer spatial scales. There is also a surprising lack of studies that have used MARXAN, despite the flexibility of this software package and its widespread use in conservation planning exercises across the globe; this may be due to Zonation's deterministic functionality making it easier for studies to make comparisons between outputs. However, in order to increase the ability of planners to incorporate PD, further work needs to be done using MARXAN, as it is a widely used tool for spatial conservation planning. In addition, the potential for surrogacy between metrics represents an understudied area within the field, and is one that perhaps has the perception of being better understood than it actually is, as there is often the misconception that spatial congruence in patterns of diversity or priority areas is sufficient evidence for or against surrogacy (Rapacciuolo et al., 2019).

It is also worth noting, in the context of the chapters that will follow, there are potential issues, within any PD-based approach, of phylogenetic uncertainty. The quality of the information that is used to create a phylogeny, which forms the basis of PD-led analyses, will impact the overall shape (= branching pattern and branch lengths) of the phylogeny; this leads to what is termed ‘tree uncertainty’ (Rodrigues et al., 2011). However, Rodrigues et al. (2011) found that, while better data leads to a better basis for conservation, decisions based on incomplete data are remarkably robust across different levels of degrading quality. Taxonomic revisions at the species level influence the shape of phylogenies – specifically, by leading to changes in the number of tips in a species-level phylogeny, and therefore may influence spatial conservation plans that incorporate PD. Of course, species-level taxonomy will also undoubtedly influence species richness-based planning. In a recent paper titled ‘Taxonomy anarchy hampers conservation’, Garnett and Christidis (2017) expressed concerns regarding the difficulties taxonomic changes represent for biodiversity conservation. There was a heated response to this by Thomson et al*.* (2018), a paper with 183 co-authors, asserting that Garnett and Christidis (2017) were mistaken in their description of the taxonomic process, and what was described as ‘Taxonomic anarchy’ by Garnett and Christidis (2017) is in fact taxonomy based on science and it is necessary for global conservation. Nevertheless, further research should be carried out to analyse the influence of taxonomic changes, such as increased “splitting” or “lumping” of species, on PD-based spatial conservation planning, as this could have important impacts on biodiversity conservation.

The incorporation of PD within spatial conservation planning is an important step in the advancement of biodiversity conversation in an increasingly resource limited world, but the field is young, and much work is still needed to further optimise the conservation of evolutionary history.

CHAPTER 3 CONSERVING THE PRIMATE TREE OF LIFE: PHYLOGENETIC DIVERSITY-BASED CONSERVATION PLANNING REVEALS SPATIAL MISMATCHES WITH A SPECIES-BASED APPROACH AS WELL THE POTENTIAL FOR SPECIES RICHNESS TO ACT AS A SURROGATE METRIC FOR PHYLOGENETIC DIVERSITY

3.1 INTRODUCTION

Biodiversity is being lost globally at an unprecedented rate (Butchart et al., 2010; Pimm et al., 2014). The scale of this biodiversity decline is so great, with species extinction rates between 100-1000 times greater than typical background levels (Ceballos et al., 2017; Pimm and Raven, 2000), and so strongly linked to human actions (Ceballos et al., 2017; Chapin et al., 1997), that biodiversity loss and efforts to prevent it have long been regarded as globally important issues (Brooks et al., 2006). This is reflected in international policy with the Convention on Biological Diversity (CBD): created in 1992-3, the CBD commits its 196 signatory countries to support the global conservation of biological diversity, sustainable use of its facets, and equal sharing of its benefits (CBD Article 1. Objectives; https://www.cbd.int/convention/articles).

Spatial conservation is one of the main tools used to address global biodiversity loss (Brooks et al., 2006; Jetz et al., 2014; Margules and Pressey, 2000; Pollock et al., 2015). The creation of protected areas that maximise representation and persistence of biodiversity, while also being able to account for other interacting factors such as those relating to socio-economics, is one of the main tools of spatial conservation (Margules and Pressey, 2000). Resources such as available area and the funds needed to cover the cost of protection are almost always limited, and maximising conservation effectiveness with limited resources is therefore a major focus of modern conservation efforts (Sandbrook et al., 2019). This issue of limited resources is exacerbated by the uneven distribution of biodiversity and its threats, with many biodiversity hotspots often situated within developing countries where resources are likely to be more limited, and where biodiversity conservation may feature far lower on the list of national priorities than in more developed countries (Brooks et al., 2006; Sutherland et al., 2017; Waldron et al., 2013).

Given that conservation almost always operates with limited resources, there is a need to prioritise those resources. One way this can be achieved is to assign species a “value”, and to devote greater resources to protecting more “valuable” species. This value can be based on economic and ecological utility, or it can be based on some measure of biological ‘uniqueness’ or ‘distinctiveness’; the latter include metrics such as phylogenetic diversity, evolutionary distinctiveness, and functional diversity (Henriques et al., 2020; Jetz et al., 2014; McNeely et al., 1990; Noss, 1990). Faith (1992) argued that more evolutionarily distinct species are expected to make larger contributions to the overall measure of diversity; this occurs if species are replaced as the basic units of diversity by features of species. Phylogenetic diversity (PD) is a metric that is intended to capture this key aspect of biodiversity, and is based on the observation that different taxa, such as species, are not equal in the amount of diversity (measured as evolutionary history) that would be lost if they were to become extinct (Faith, 1992). The PD of a taxon (such as a species or set of species) is calculated as a the sum of the unique phylogenetic branch lengths (typically in units of time, such as millions of years) that connect that taxon to the root of a given phylogeny in which it is present, and thus indicates their contribution to the tree of life (Faith, 1992). PD has been associated with ecosystem function and stability (Cadotte, 2013; Cadotte et al., 2012; Forest et al., 2007) and has been cited as capturing increased adaptation potential which would increase the chance of species and ecosystem survival under changing environmental conditions (Faith, 1992, 2019; Vane-Wright et al., 1991). Not only is PD a key aspect of biodiversity, but it also provides information that can aid in the ‘agony of choice’ faced by conservationists, namely the issue of limited resources already discussed (Vane-Wright et al., 1991). This adoption of PD as core metric, over species richness, can also avoid issues surrounding taxonomic uncertainty (Rosauer et al., 2018 and see Chapter 5).

Since the turn of the century, but particularly within the last five years, studies have started to investigate the utility of PD, not only as an important facet of conservation biodiversity, but more practically in how to incorporate it within conservation strategies, and in particular within spatially optimised conservation plans (*e.g.* Brum et al., 2017; Carta et al., 2019; Polasky et al., 2001; Pollock et al., 2015; Rodrigues and Gaston, 2002). One of the most widely used approaches to conserving PD using spatial optimisation software, such as MARXAN (Ball and Possingham, 2000) and Zonation (Moilanen et al., 2012), involves decomposing a phylogeny of a given clade into its constituent branches, and mapping these branches across space based on the combined ranges of the species that descend from each branch. These branches can then be treated as individual conservation features for which bespoke coverage targets and weightings can be set using Zonation, MARXAN or similar spatial optimisation tools. The ability to set targets for every element of a phylogenetic tree allows planners to avoid underrepresentation issues associated with strategies that focus on diversity hotspots; for example, not all elements of a phylogeny *i.e.* branches of the phylogenetic tree, or any conservation feature for that matter, may be captured adequately, or at all, within a hotspot. This approach of decomposing a phylogeny into its constituent branches, mapping those branches across space, and then identifying priority areas for the protection of PD was first introduced by Polasky et al. (2001), and will be referred to in this chapter as a ‘weighted branch-based’ approach. Polasky et al. (2001) did not identify priority areas using spatial optimisation algorithms due to concerns over computational difficulties. However, Rodrigues and Gaston (2002) quickly built on Polasky et al. (2001) weighted branch-based approach by incorporating the optimisation software C-PLEX, and this then formed the basis for a series of subsequent studies that employed more specialised spatial optimisation software, typically MARXAN or Zonation (*e.g.* Carta et al., 2019; Pollock et al., 2015; Rapacciuolo et al., 2019; Rosauer et al., 2017, 2018).

To date, only a comparatively limited number of published studies have incorporated PD into a spatial conservation planning exercise (13 studies), but this number is growing rapidly (see literature review Chapter 2). Most of these studies are on taxonomically high-level clades (at or above the level of the Class in the Linnaean hierarchy) (see Table 2.2). The shortage of case studies focussing on lower-level clades means that there is limited data for planners to make informed decisions when planning for conservation scenarios that attempt to protect members of those lower-level clades. Results from these studies also vary regarding whether species richness has the potential to act as a surrogate for PD. Brum et al. (2017) found that global prioritisation areas for terrestrial mammals based on PD showed low levels of overlap with those based on species richness targets. By contrast, Rapacciuolo et al. (2019) found that, despite spatial mismatches in conservation plans, species richness-led plans captured PD well, and therefore species richness could operate as a successful surrogate for PD for terrestrial vertebrates in the Americas. However, this finding by Rapacciuolo et al. (2019) conflicts with the findings of Rosauer et al. (2017) for terrestrial mammals globally. Rosauer et al. (2017) reported that, not only were there substantial spatial differences in the priority areas for PD- versus species-based approaches, but that species was a poor surrogate for PD. However, Rosauer et al.'s (2017) results showed more specifically that levels of surrogacy were associated with the amount of available area that their chosen optimisation tool, MARXAN, was constrained to, with poor surrogacy at lower levels of available area and increased surrogacy when area was less constrained.

Much more work is needed in the field of PD-led spatial conservation planning, in order to understand how it performs in comparison to planning that uses other metrics, such as species richness. This chapter presents a case study that uses the global range of (non-human) primates to investigate these questions. Primates are a particular conservation focus (Marshall and Wich, 2016), with many species endangered due to a variety of threats, including hunting, disease, climate change, and the loss, degradation, and fragmentation of their habitats. This is particularly concerning as primates play an important role in many key ecological functions (*e.g.* pollination, seed dispersal, carbon sequestration, etc.) (Marshall and Wich, 2016). As well as this, many primate species are charismatic and have high cultural value and public appeal, and Primates is the order to which humans ourselves belong; as a result, primates can serve as flagship species whose protection, and increased awareness, can benefit other species and habitats. Many primate species are also considered indicator species, with the health of their populations reflecting the general health of an ecosystem (Marshall and Wich, 2016). Primates also represent an excellent model group to study spatial patterns of phylogenetic diversity, as their ranges are comparatively well studied and documented, and their species-level phylogeny is well understood (*e.g.* dos Reis et al., 2018; Faurby and Svenning, 2015; Springer et al., 2012).

In this chapter, a weighted branch-based PD approach is applied to a conservation planning exercise for 310 extant non-human primate species, considering differing amounts of available area. The approach is adapted from Rosauer et al. (2017), but with a novel approach to calculating the distribution of branches that creates maps for the distribution of branches, as opposed to multiplying matrices. Alongside the weighted branch-based approach, a parallel analysis was run using species-based targets. The major aims of this chapter are to identify priority areas for the conservation of primate evolutionary diversity, compare these priority areas to those identified using a species-based approach, and to compare the amount of PD captured by each approach to test whether species richness could act as a suitable surrogate for PD.

3.2 METHODS

3.2.1 SPATIAL DATA

Expert range maps for all extant non-human primate species (henceforth referred to as "primates") for which these were available were extracted from the IUCN's database as a shapefile (IUCN, 2019). An equal area grid (Behrman projection) of 110km^2 (1° at the equator) was created over the fullest extent of range maps, *i.e.* the combined range of all primates for which maps were available, with each cell of the grid representing a planning unit; this resulted in a total of 4429 planning units. The grid was clipped exactly to the combined primate range map; thus, where a planning unit was intersected by the coastline or by areas with no data, it was clipped to this intersection and therefore had an area of less than 110km^2, resulting in a more accurate account of species ranges when compared to approaches that do not account for exact planning extents (*e.g.* Brum et al., 2017; Rosauer et al., 2017).

3.2.2 PHYLOGENETIC DATA

Phylogenetic data for primates was represented at the species level through the most recent time-calibrated phylogeny (or “time tree”) for primates available, taken from dos Reis et al. (2018). This phylogeny builds on work by Springer et al. (2012) and includes 372 species (367 primates and 5 outgroups, 3.4 million aligned base pairs). Manual taxonomic alignment between the species for which phylogenetic data was available and the species for which spatial data was available resulted in a final dataset of 310 species with spatial and phylogenetic data across the 4429 planning units.

3.2.3 BRANCHES AS CONSERVATION FEATURES

The approach of using branches as conservation features used here is based on Rosauer et al. (2017), who built on work by Rodrigues and Gaston (2002). The key element of this approach, as far as conserving PD is concerned, is identifying the geographical range of every branch in the phylogeny (both internal and terminal), and then weighting the branches by their length (*i.e.* the amount of evolutionary history they represent) in a spatial optimisation algorithm; each weighted branch is treated as an individual conservation feature that can have individual coverage targets.

Here, the geographical range of each branch at any level on the phylogeny is determined by the union of the range of the tree tips (*i.e.* the species) that descend from that branch. The intersection of these ranges with the planning grid is then used to determine the exact amount of each branch within each planning unit and can subsequently be used to set individual targets in a spatial conservation planning exercise. In more detail, the process is as follows: Firstly, the phylogeny is used to identify every tip (*i.e.* species in a species-level phylogeny, as is the case with the primate phylogeny here) that descends from each node (bespoke function ‘*every tip per node*’ written within R see Appendix I.)). This produces a matrix of every tip per node within the tree. This matrix is then used in combination with the spatial ranges of the species (in a shapefile); the ranges of the tips (species) that descend from each node are combined via a union; this new range is written as a new shapefile (bespoke function '*get unions from every tip per node'* written in R, see Appendix II.)). For the primate phylogeny used here, this resulted in 309 new shapefiles, representing the spatial range of the 309 internal nodes of the phylogeny, which were added to the range of the individual species (n=310), resulting in a total of 619 shapefiles. Intersecting these shapefiles with the planning grid provided the range of each branch within each planning unit. This information was used to create a MARXAN input file (puvsp.dat) that tells MARXAN how much of each conservation feature is in each planning unit (see Figure 3.1 for a breakdown of this process).

The primary difference between the approach here and that presented by Rosauer et al. (2017) is the way the occurrence of a branch is calculated within each planning unit. Rosauer et al. (2017) used the proportion of each planning unit occupied by a species as a measure of occurrence; however, when multiple descendants of a branch occur in the same planning unit, they summed the areas occupied within the planning unit, up to the total area of the planning unit. Creating individual ranges for each branch, as done here, avoids the need to sum occurrences in this way, and represents an alternative approach to building the input files for the prioritisation of PD using branches. Nonetheless, both approaches would result in the same outcome *i.e.* the same occurrence data for each branch in each planning unit.

MARXAN's objective function attempts to minimise the cost of the protected areas while meeting conservation targets. Within this, there is a feature penalty factor which can be used to assign varying levels of importance to different conservation features within the prioritisation; the larger the feature penalty, the more important the conservation feature (Ball et al., 2009; Ball and Possingham, 2000). Here, the feature penalty factor (referred to as the 'species penalty factor' within MARXAN) is used to maximise PD within the conservation plan. Each branch is assigned a weight that is proportional to its length in millions of years (Rosauer et al., 2017). Longer branches have higher penalties and are therefore more important; thus, they should be favoured for protection over shorter branches. Each branch, weighted in proportion to its length, can only be counted once within a planning unit, regardless of the number of descendant tips present. Therefore, the planning software does not need to deal with the hierarchical relationship between phylogenetic branches.

3.2.4 TARGET SETTING

As in Rosauer et al. (2017, 2018), and similarly to other previous global studies (Rodrigues et al., 2004; Venter et al., 2014), a bounded percentage strategy was used to set representation targets for conservation features, with the same target of 25% of the range of species and branches (including internal and terminal branches) being used. To prevent the results being dominated by widely distributed conservation features, primarily deep branches in the phylogeny that will represent a large majority of the total range of the 310 species, or underrepresenting rare endemic species, the targets were constrained to a maximum of the equivalent area of 25 planning units, and a minimum of 1 planning unit, or the maximum range of a feature if its total is less than 1 planning unit, as was also done by Rosauer et al. (2017).

3.2.5 SPATIAL OPTIMISATION

MARXAN (ver. 2.4.3; Ball and Possingham, 2000) was used to optimise the selection of areas, identifying the planning units that represent the lowest cost to achieve the targets set, or (if this cannot be achieved) as close to the targets as possible. The cost of protection, within MARXAN's objective function, was set as proportional to the amount of area selected for protection, as is standard practice when no real-world cost data is available (Ardron et al., 2010). For each set of targets, MARXAN was run 200 times, with an annealing control of 100,000 iterations, following the principles of good practice in the MARXAN Good Practices Handbook (Ardron et al., 2010). Selection frequency (the number of times a planning unit was selected in one of the 200 runs) was used to identify major differences between the outputs of the two approaches. MARXAN's objective function allows for the incorporation of connectivity via a Boundary Length Modifier (BLM) which weights the amount of fragmentation allowed within solutions. While the BLM facilitates the inclusion of connectivity, an important ecological concern for stakeholders, it reduces the ability for comparisons between the MARXAN outputs of different approaches and is therefore set to 0 in all runs here and throughout the research chapters in this thesis.

If MARXAN is allowed to consistently achieve all its targets, PD would be protected without directly considering it: this is because, if MARXAN is not forced to miss some of its targets, it does not have to employ the species penalty factor, which is critical to PD being prioritised within this approach. So, in order to ensure PD was always considered during the optimisation process, the amount of area available to conserve was deliberately limited. This was achieved by using MARXAN's 'cost threshold'. As the name indicates, this input variable sets a threshold for the total cost (in this case, the amount of area) beyond which MARXAN will not exceed, provided the cost is set high enough (Ardron et al., 2010). MARXAN could meet all its targets in this approach within 15% of the total global range of primates (Figure 3.5). Cost thresholds were therefore chosen to represent different area constraints below this, decreasing in 2.5% increments from 15% down to 2.5% of the total available area. The cost threshold penalty for each scenario, *i.e.* percentage or range, was optimised to the lowest value that would limit the cost to the specified threshold, in this case representing an amount of area; the cost threshold represents the amount of land that is available to MARXAN, and the species penalty, if set high enough, ensures that MARXAN does not exceed this amount of land. The requirement for the cost threshold to be as low as possible ensures that the search process can find better solutions around the cost threshold. This deliberate restriction of area available also reflects the wider issues driving PD based conservation, namely that resources are limited and that PD provides a suitable metric for deciding on prioritisations when there is the 'agony of choice' (Vane-Wright et al., 1991).

3.2.6 SPECIES-BASED APPROACH

The weighted branch-based PD approach to spatial prioritisation presented here was also compared to a more "traditional", species-based approach. This was achieved by carrying the same analysis as the weighted branch-based method but removing the range of the internal branches and just using the tips (*i.e.* the species), and setting the species penalty factor to a uniform, calibrated, figure; this is calibrated iteratively so that it is not so high that is restricts MARXAN's performance, but not so low that targets are frequently missed (Ardron et al., 2010). This same calibration formed the initial basis for the species penalty factor for the branches in the branched based approach from which proportional (to the length of each branch) penalties were calculated. As in Rosauer et al. (2017), equivalently calibrated weightings allowed for subsequent comparisons between approaches.

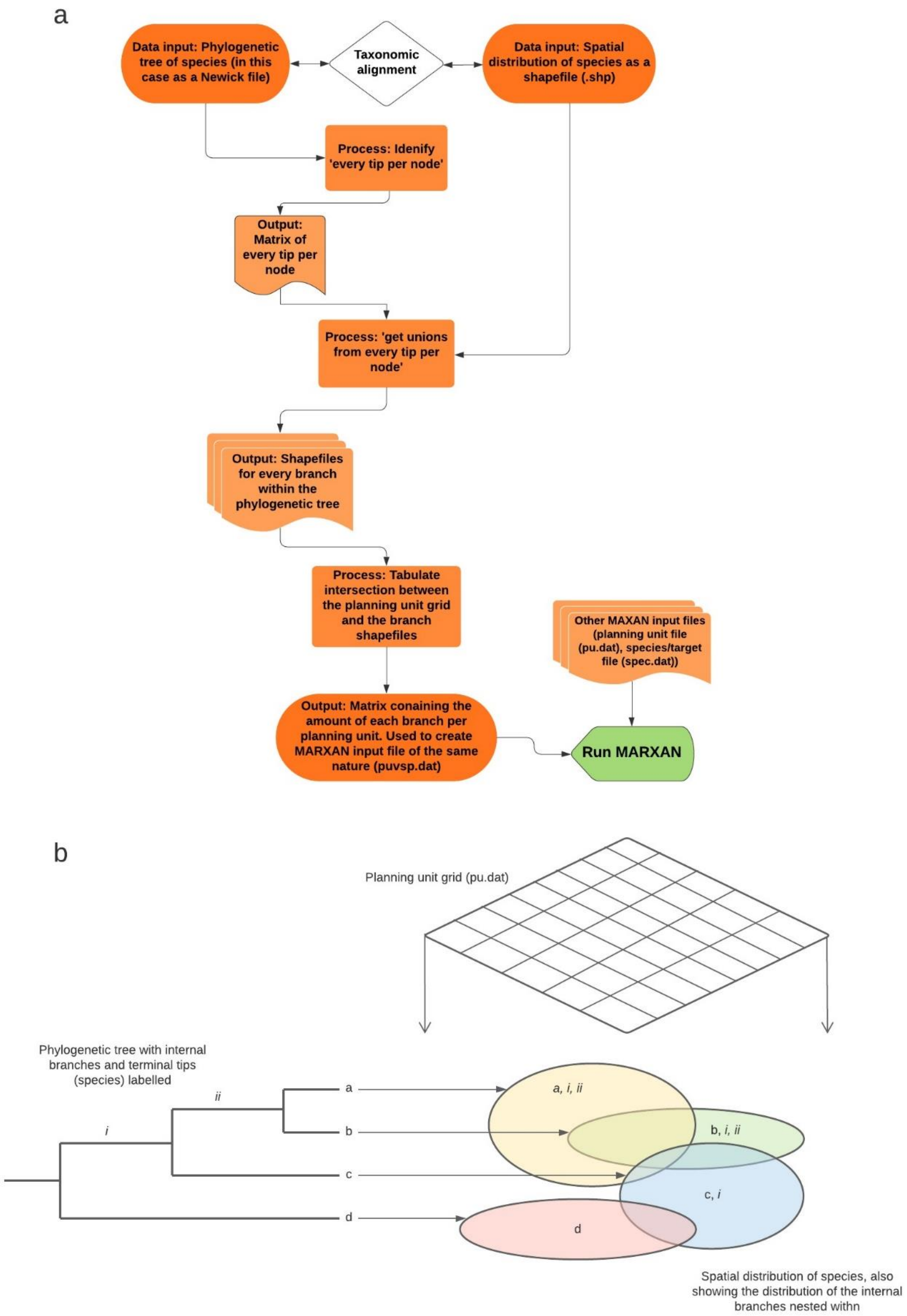

Figure 3.1 Breaking down the phylogeny of a clade. Each branch becomes an individual conservation feature with its own range, for which coverage targets can be set. a.) a simplified workflow for building individual shapefiles for each branch and then calculating their occurrence across a planning area divided into planning units. b.) visual representation of the concept of internal branches having their own range based on the combined range of their descendant species.

3.3 RESULTS

3.4 LOCATION OF PRIORITY AREAS

Priority areas for the conservation of primate PD were identified using MARXAN with a weighted branch-based approach. Differences in the location of priority areas were found between the weighted branch-based approach compared to the species-based approach. These became more pronounced as area restriction increased, *i.e.* as the amount of area available decreased (Figure 3.2). This disparity increases in a relatively consistent fashion as the area becomes more limited (Figure 3.2). The most substantial differences were seen when the amount of area available was limited to the lowest value used here, namely 2.5% of the total available (Figure 3.2 and Figure 3.3). Although there is still a weak correlation, in terms of the selection frequencies, between the weighted branch-based and species-based approaches, at 2.5% the differences occur at high selection frequencies (*i.e.* at the upper limits of the *x* and *y* axes in Figure 3.2), meaning that the greatest differences occur at the highest levels of prioritisation. The selection frequencies become more similar for each planning unit as the amount of area available increases. However, differences in highly selected areas between the two approaches are still present all the way through to, and including, when the area available reaches 12.5%. Both approaches could meet all of their targets, *i.e.* with no restrictions on available area, within the same amount of area (~15% of the total range of primates), and when this was done no major difference was found between the priority areas selected. This is expected as internal branches are nested within the range of species (*i.e.* if every tip/species meets its coverage target then every internal branch will also inherently be captured) and when all targets are allowed to be met then MARXAN will not use the feature penalties, in this case used to account for differences in PD, and as a result PD will not be actively conserved (Figure 3.2 - 'No Cost Threshold').

The spatial implications in these differences can be seen in the maps shown in Figure 3.3 and Figure 3.4. Pronounced differences can be seen at the 2.5% area constraint in South America, where there are areas which are much more highly prioritised in the weighted branch-based approach compared to the species-based approach (Figure 3.3). The converse can be seen in the same 2.5% map, where there are areas which are more highly prioritised in central Africa for the species-based approach (Figure 3.3). The more homogenous selection of areas is reflected in the maps for the less constrained 10% area output (Figure 3.4).

On a regional and species scale, the results show differences between approaches, particularly when area is constrained the most. At the 2.5% area, of the 57 species that met their coverage targets under the species-based approach, four species were critically engendered, according to the IUCN Red list classicisation, zero of which were Old World monkeys. This is compared to the PD approach where, within the 56 species that met their targets, twice as many (n=8) critically endangered species were captured, half of which were Old World monkeys.

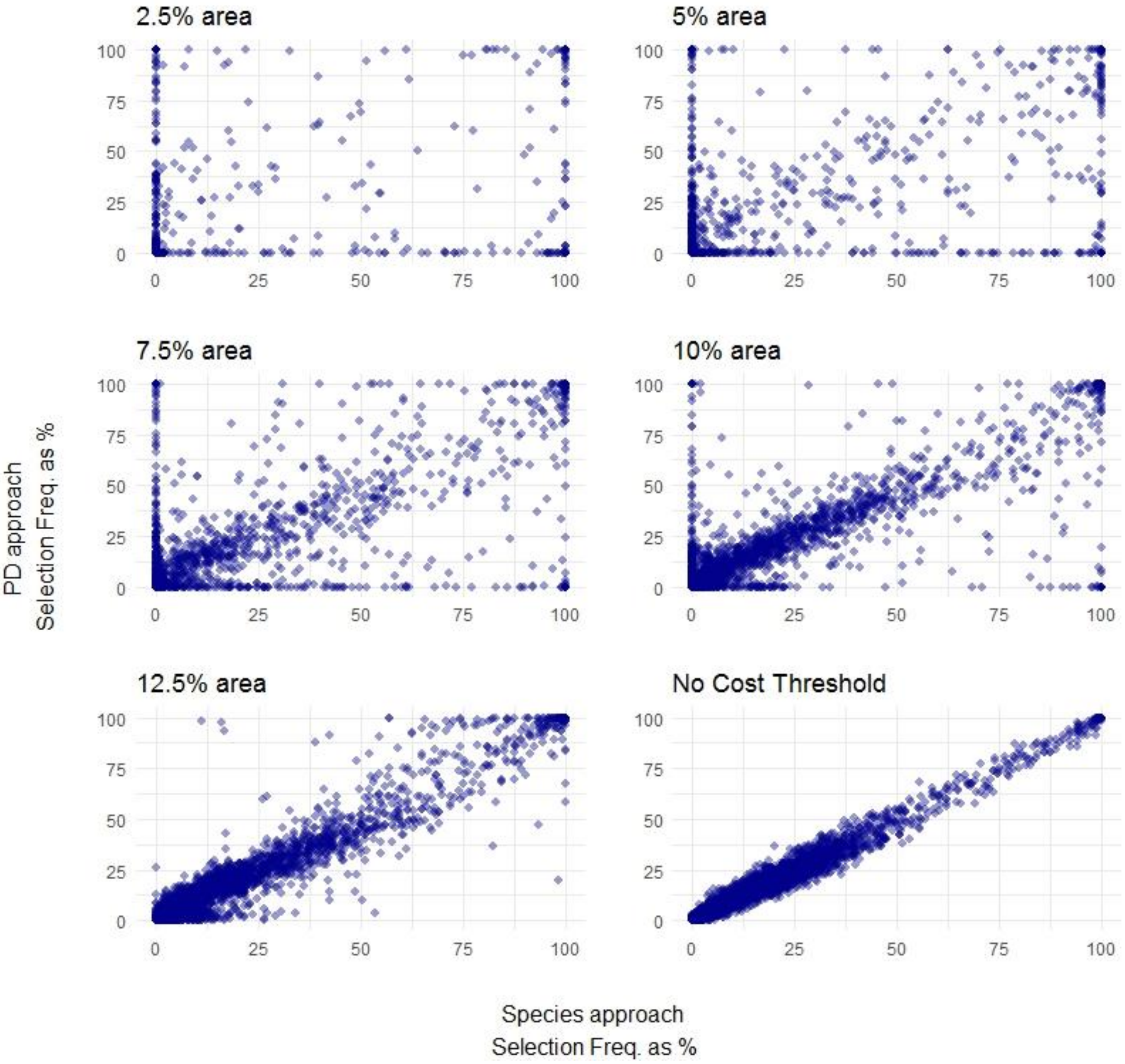

Figure 3.2 Selection frequencies (as a percentage (n=200 runs per optimisation)) for every planning unit (n=4429) for each MARXAN optimisation at each area constraint for both PD (weighted branch-based target setting) and species lead (equally considered species-based target setting) approaches.

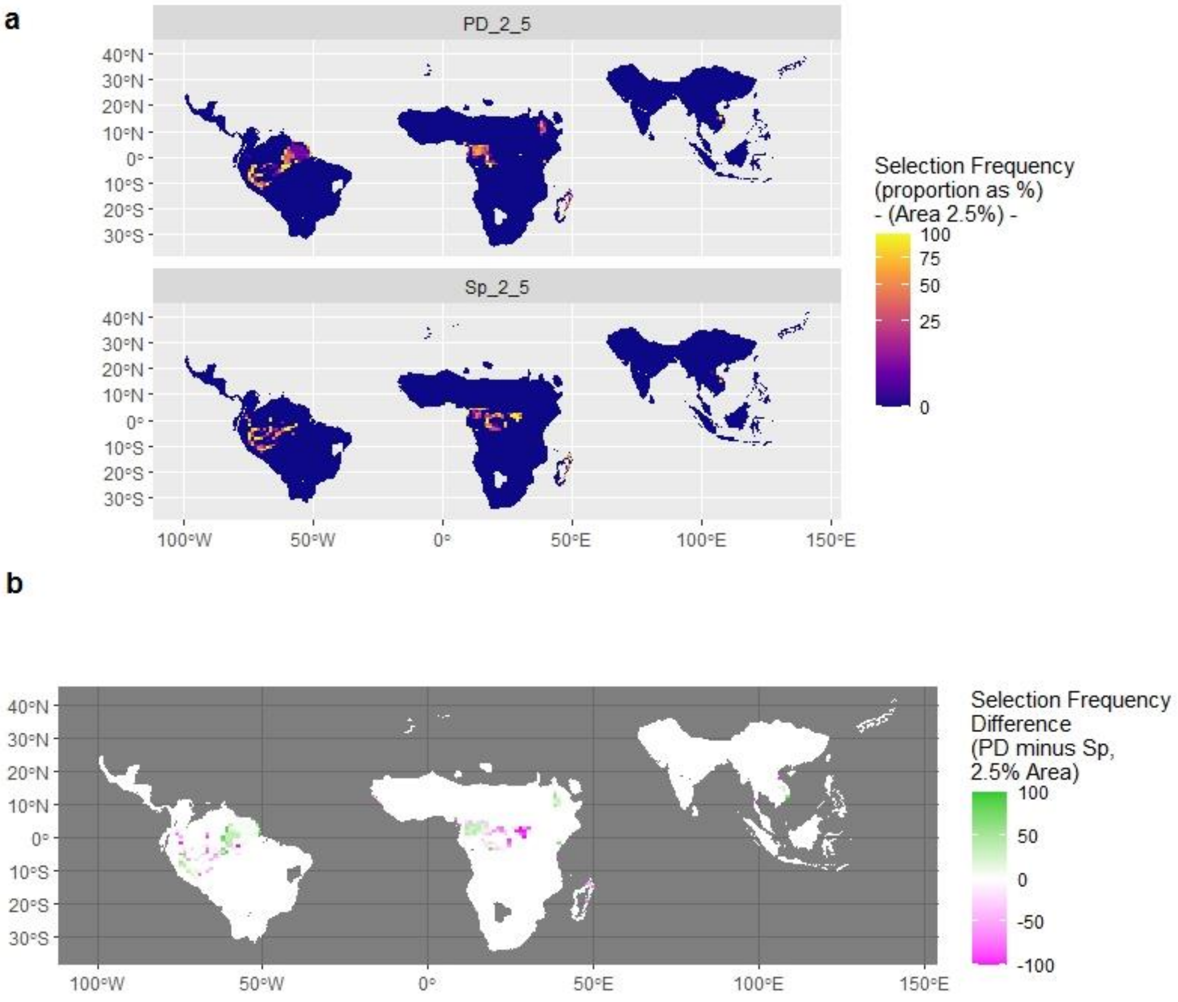

Figure 3.3 Priority areas for conserving primate phylogenetic diversity and species richness (and the differences between the two) when the area available is limited to 2.5% of total primate range. Priority areas are identified through MARXAN's selection frequency with 200 runs. a.) PD_2_5 the selection frequency from the weighted branch-based approach using PD (weighted branch-based target setting) and Sp_2_5 shows the selection frequency from the species-based approach (equally considered species-based target setting) b.) a difference map highlighting the areas where the two approaches differed, with the stronger colours indicating where the approaches differed the most (green for areas more favoured by the weighted branch-based approach and purple for those areas more favoured by the species-based approach)

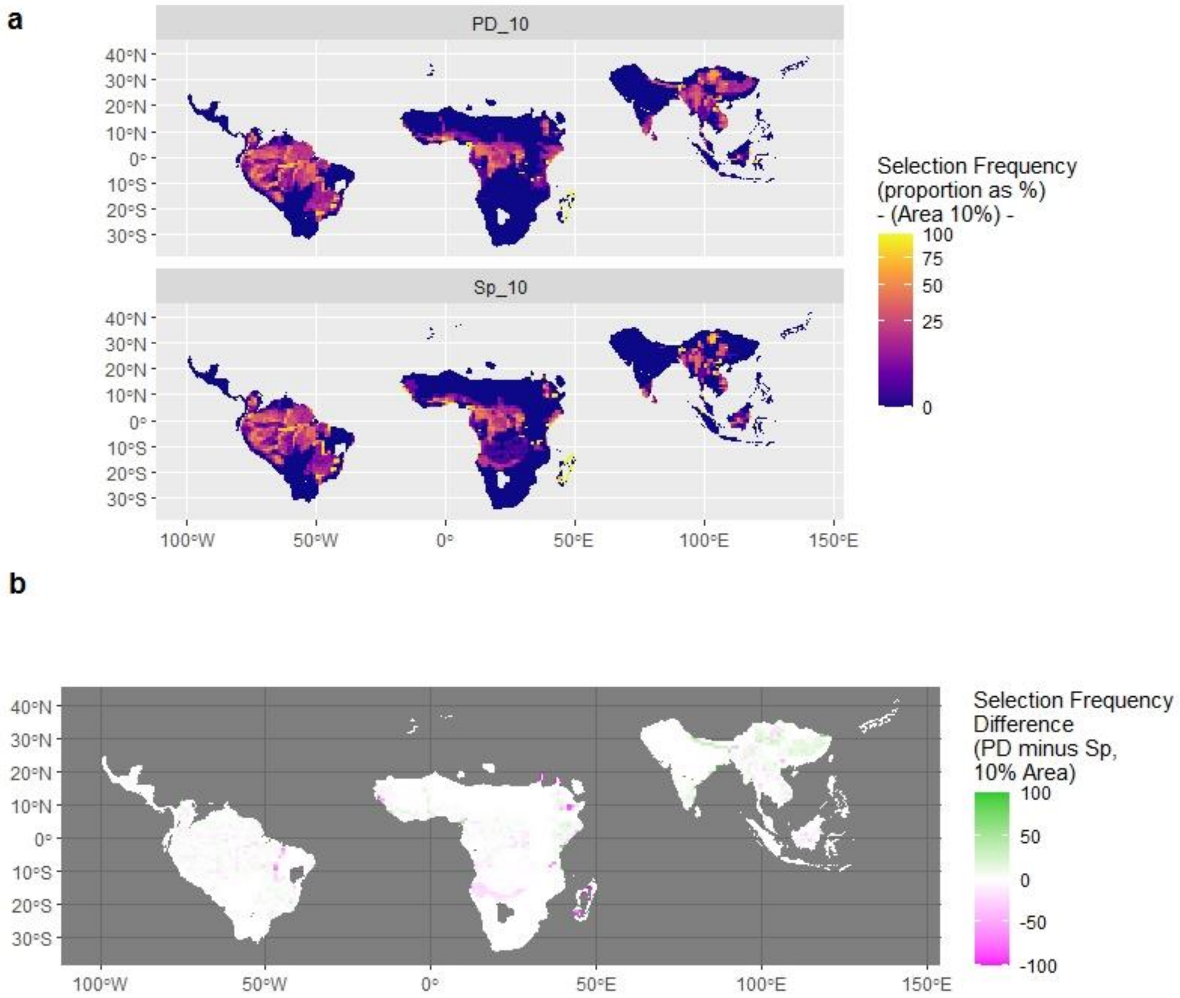

Figure 3.4 Priority areas for conserving primate phylogenetic diversity and species richness (and the differences between the two) when the area available is limited to 10% of total primate range. Priority areas are identified through MARXAN's selection frequency with 200 runs. a.) PD_10 the selection frequency from the weighted branch-based approach using PD (weighted branch-based target setting) and Sp_10 shows the selection frequency from the species-based approach (equally considered species-based target setting) b.) a difference map highlighting the areas where the two approaches differed, with the stronger colours indicating where the approaches differed the most (green for areas more favoured by the weighted branch-based approach and purple for those areas more favoured by the species-based approach)

3.5 AMOUNT OF PD CAPTURED

No major difference was found in the amount of primate PD captured within the weighted branch-based approach compared to the species-based approach; this was the same across all levels of area restriction (Figure 3.5a). Although the weighted branch-based approach consistently captured more PD, which was expected, the difference was small at each level of area restriction, averaging ~0.5% and peaking at ~2% PD when the area was constrained to 10%. Both approaches showed an approximately logarithmic relationship between area and amount of PD captured, with 100% of PD captured within ~15% area.

No major difference was found in the number of species captured between weighted branch-based or species-based approaches (Figure 3.5b). A linear relationship between area and number of species captured was found for both approaches. The species-based approach captured more species than the weighted branch-based approach at 5%, 7.5%, and 10% area, with the difference greatest at 10% area (21 more species).

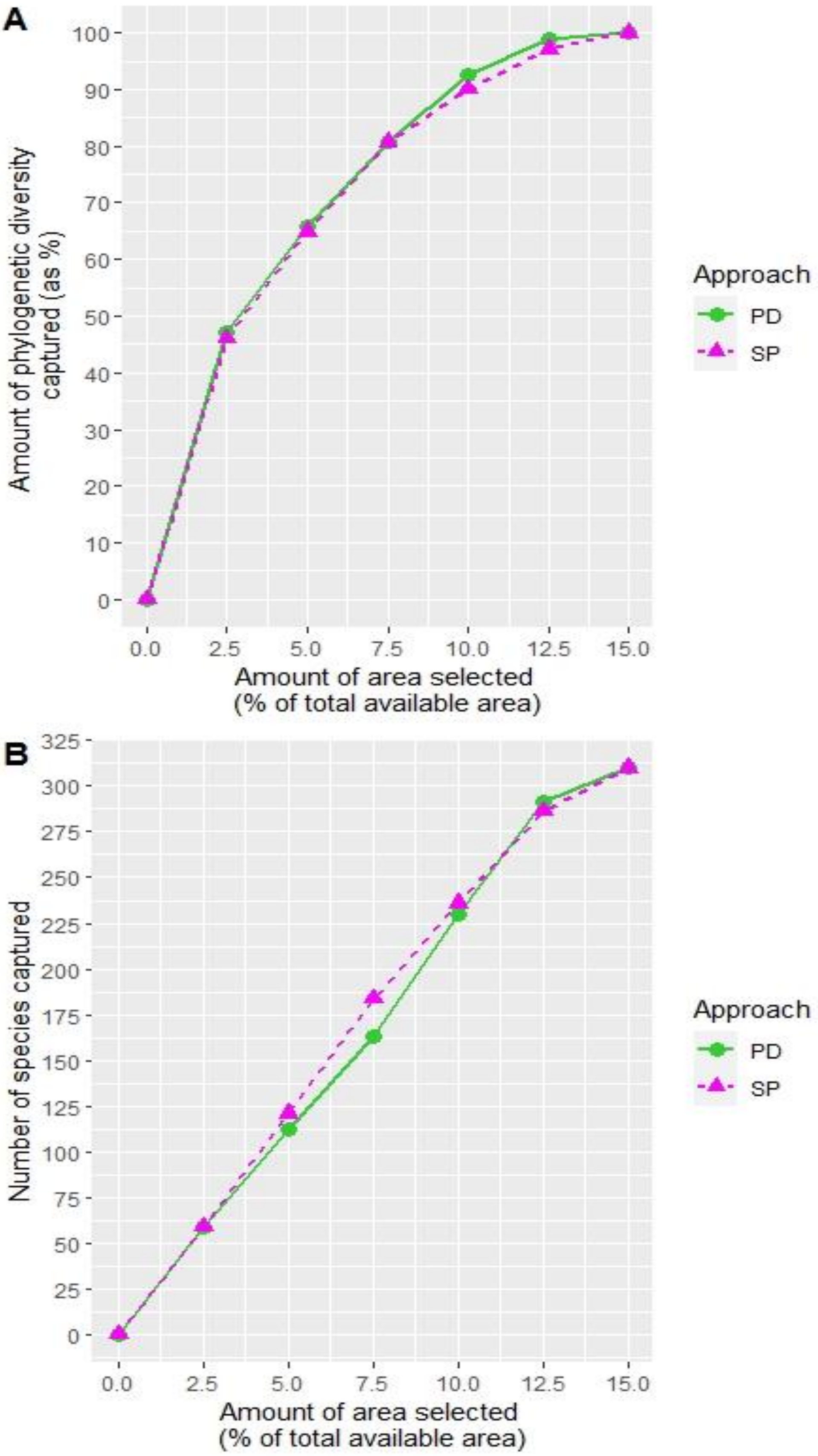

Figure 3.5 The amount of PD (a) and number of species (b) captured by each approach to target setting (PD = weighted branch-based approach, SP = species-based approach) at each level of area constraint.

3.6 DISCUSSION

The results of this chapter identify priority areas for the conservation of primate evolutionary history. More specifically, this is the first study to identify priority areas for primate evolutionary history using a spatial optimisation tool, in this case MARXAN. This chapter is a valuable case study for the relatively new weighted branch-based method for conservation of PD. The parallel species-based analysis allowed for comparisons to be made between the amount of spatial overlap between the two approaches, as well as the amount of PD captured by prioritisations based on species richness alone, providing insight to the idea of surrogate metrics. Overall, spatial mismatches were found between the two approaches; these mismatches increased as the amount of available area decreased. However, there was little difference found between the two approaches when it came to the amount of PD they captured, suggesting that, for primates, species richness may in fact be a good surrogate for PD.

3.6.1 SPATIAL MISMATCHES

The results of the MARXAN runs when the amount of available area was not limited (No Cost Threshold set) showed no major difference between the weighted branch-based and species-based approaches. This was expected due to the way MARXAN operates (as explained in the methods section 3.2); if MARXAN is allowed to meet all its targets for the tips of a phylogeny (species in the case of a specie-level phylogeny), then all the targets for internal branches are inevitably met as well, without taking into account the differing amounts of PD they represent. This is an important factor of this approach; PD is only accounted for if MARXAN is stopped from meeting all its targets. Under a real-world example the amount of available land is likely to be limited, meaning MARXAN would not be able meet all its targets, and so PD would be accounted for. However, if this is not the case, and MARXAN can meet every one of its targets, planners may assume that PD has been accounted for in the most optimum manner, when in fact the protection of PD in this scenario would be passive and there may be hidden and therefore missed areas of PD. These areas of missed PD would be revealed if a small amount of spatial constraint is applied in the planning process. This is exemplified in the results in this chapter in the differences in the selection frequencies that are seen with application of just a 2.5% reduction to the 'No cost threshold' (at 15% area, where MARXAN can achieve all targets), as seen in the 12.5% example; the addition of a slight restriction results in noticeable differences in the selection frequencies between the weighted branch-based and species-based approaches. It is important for conservation planners to understand how constraints and thresholds on approaches that include prioritisations through the application of penalties, as in the weighted branch-based method used in this chapter, to ensure their aims are met.

Under limited resources (specifically, when available area was limited) spatial mismatches were found between prioritisations based on PD when compared to those that were species-based. This is something that has been universally found in published studies (Carta et al., 2018; Lindegren et al., 2018; Wong et al., 2018; Zupan et al., 2014, also see literature review Chapter 2): to a greater or lesser degree, all the studies that have compared optimisations for PD with those based on species richness have found spatial mismatches between the areas identified (Brum et al., 2017; Pollock et al., 2017). Brum et al. (2017) reported high levels of spatial mismatch between priority areas for the conservation of global mammal species richness compared to PD, calculated using phylogenetic eigenvectors. This spatial mismatch was also reflected in the findings of Rosauer et al. (2017) and their weighted branch-based approach to the conservation of global mammal PD, when compared to one using species-based targets. In addition, Pollock et al. (2017) showed that, while there were similarities between PD- and species-based approaches in the location of the priority areas for the conservation of the world's bird and mammal species, the choice in strategy had a fundamental effect on the location of priority areas identified. Spatial mismatches in PD-versus species-based prioritisations, such as those found in this chapter and elsewhere in the literature, present a strong case for the inclusion of PD in spatial conservation planning approaches that aim to conserve evolutionary history. However, it should be noted that some authors have questioned whether a focus on PD is beneficial to the conservation of biodiversity (Cantalapiedra et al., 2019; Tucker et al., 2019). Cantalapiedra et al. (2019) found that on a macroevolutionary scale, using 10 dated species-level palaeo-phylogenetic trees that ranged from Foraminifera to dinosaurs, prioritisations that were based on conserving PD generally resulted in fewer subsequent linages when compared to a prioritisation approach that gave preference to diversifying lineages. Tucker et al.'s (2019) work on the other hand calls into question the efficacy of PD to capture phenotypic diversity, both measured and unmeasured, alongside the variation in the evidence for the benefits associated with protecting phenotypic diversity in relation to ecosystem services. Tucker et al. (2019) calls for more work to fill in some of the knowledge and evidence gaps when it comes to identifying important metrics for effective conservation.

While, similarly to work by Rosauer et al. (2017), it was the main focus of this chapter to focus on the global picture of PD-based versus species-based spatial conversation, there are some interesting finer scale elements of the results that could help to direct further work. The difference in the number of critically endangered species, as well as the proportion of these that are Old World monkeys, brings to the fore the wider impact of different approaches to spatial conservation planning, particularly when it comes to the inclusion of PD. The uneven spread of the threat of extinction across the tree of life, with more evolutionary distinct taxa being at more risk of extinction (Purvis et al., 2000), may be reflected in this chapter where more critically endangered species were captured by the PD-based approach, when resources (*i.e.* area) were most limited, compared to the species-based approach; the addition of a measure of evolutionary distinctiveness (a measure of how isolated a species is within a clade (Vane-Wright et al., 1991)) would aid in the identification of more at risk species. This serves to show, not only the importance of considering PD in spatial conservation planning, but it also reflects the need for decision making processes which take into account multiple interconnected metrics that are important to the conservation of biodiversity, and that do not assume surrogacy or the completeness of an approach. Another finer scale result of note here is the increase in the number of critically endangered Old World monkeys captured between the approaches, with the PD-based approach capturing more of these species than the species-based approach; while only slight, this may be indicative of higher levels of taxonomic splitting occurring in New World monkeys. This may further indicate the power of PD-based conservation as it has been cited as being more resilient to such taxonomic changes, compared to more species-based approaches; this, as well as the further implications of taxonomic changes to spatial conservation forms the basis of the work in Chapter 5.

An important result of this chapter is the relationship between the amount of available area and the amount of mismatch between weighted branch-based and species-based approaches. The results here show that the limitation of resources, in this case area, has a substantial effect on the difference in the location of priority areas between weighted branch-based and a species-based approaches; specifically, the larger the constraint, *i.e.* the smaller the amount of available area, the greater the difference in the selection frequencies of each planning unit between the approaches. The same trend was found by Rosauer et al. (2017) when looking at the global distribution of mammals, but has not reported elsewhere in the literature. However, other major studies have focussed on a fixed amount of available area, which may explain, in part, the variation in the amount of overlap in the areas selected by the two different approaches reported in these other studies (Brum et al., 2017; Pollock et al., 2017).

It is important to understand, and to take into account, the role that constraining an approach has, particularly when placing a constraint is key to how a metric is included - *e.g.* the use of cost thresholds here to ensure MARXAN has to use penalties and PD is therefore accounted for. Under high area constraints, PD-based solutions will contain a greater proportion of more evolutionarily distinct species (*i.e.* that lack close relatives), whereas species led-approaches remain agnostic to evolutionary history at all levels. The differences between PD- and species-based approaches will become less stark as the area constraints are set closer to the level where all targets can be met (in this case 15% area).

3.6.2 SPECIES AS A SURROGATE FOR PD

Despite the varying spatial mismatches in the priority areas identified, it is striking that the amount of PD captured does not vary markedly between the weighted branch-based and species-based approaches at all levels of available area (between 2.5 and 15% of the area available, increasing in 2.5% increments). This result suggests that species richness may have the potential to act as a suitable surrogate for capturing PD, at least for the clade considered here, namely Primates. More work is needed to investigate this finding further, as other studies have reached differing conclusions on this issue (Rapacciuolo et al., 2019; Rosauer et al., 2017). It may be the case that, within Primates, there may not be much variation in the amount of PD that each species represents (at least compared to the groups examined by Rosauer et al. (2017)), and thus there is little difference in the amount of PD captured by the species-based approach when compared to the weighted branch-based approach. This idea of the composition of a phylogeny being important to PD based conservation planning is explored further in Chapter 4.

The idea that species-based conservation plans can adequately capture PD, and therefore act as a surrogate metric, has been questioned by studies that have investigated the patterns of phylogenetic and species richness and found incongruences between the two (Devictor et al., 2010; Pardo et al., 2017). These findings have driven studies to investigate the difference between priority areas for the conservation of PD and species richness using optimisation algorithms and focussing on the amount of overlap between the priority areas identified, citing substantial differences between the two approaches, as found here and discussed above (Brum et al., 2017; Pollock et al., 2017). However, the measure of surrogacy is not in the amount of overlap between priority areas, as has been reported by some (Rodrigues et al., 2011; Rodrigues and Brooks, 2007), but rather in the amount of one metric (*e.g.* PD) that is captured within a plan designed to capture another (*e.g.* species richness) (Rapacciuolo et al., 2019). When this measure of surrogacy was applied in this chapter, a high level of surrogacy was found for PD captured by species-based prioritisations. High surrogacy was also reported in the work by Rapacciuolo et al. (2019) who investigated the potential for species richness to act as a surrogate for PD in terrestrial vertebrates (n=10,213) across the Americas, using the same weighted branch-based approach to the conservation of PD, but a different prioritisation software (Zonation, rather than MARXAN, as was used here). However, Rosauer et al. (2017) found that, while there were high levels of PD captured by a species-based prioritisation when the amount of available area was less restricted, this reduced dramatically as the amount of available area decreased. This is contrary to the findings of this chapter, where the amount of PD captured by the species-based prioritisation varied little between area restrictions.

Given that the same approach used by Rosauer et al. (2017) was applied in this chapter, the differences are likely to arise from the data. The main reason proposed here is that, on average, primates have smaller and more overlapping ranges than when considering all terrestrial mammals together. These comparatively smaller and more overlapping ranges of primates result in larger amounts of PD being captured when using a species-based approach when compared to all terrestrial mammals, as in Rosauer et al.'s (2017) case study, although this requires further investigation. Nevertheless, the results from this chapter add to the idea that species richness can act as a suitable surrogate for PD, although as mentioned before this may be clade-specific. However, such potential surrogacy should always be viewed with caution, as anything that is accounted for passively, like PD in a species-based conservation plan, allows for the possibility that PD will be sub-optimally accounted for. For example, a species-based conservation plan for a clade that has areas of high species richness may be able to capture seemingly adequate levels of PD within a small area purely due to the high numbers of species present; but this plan may fail to protect large parts of the clade’s phylogeny, represented by any of the species that are not included the priority area, as the approach is completely agnostic to evolutionary relationships. Further to this, not all studies of surrogacy, or (more broadly) spatial conservation in general, are comparable, with spatial mismatches potentially resulting from methodological differences. For example, the size of the units in a study can impact the amount of overlap found, as richness patterns are often scale-dependent (*e.g.* Rahbek, 1995). The results from this chapter also show the large impact constraining the available area in a MARXAN approach can have when the key element to be conserved (PD) is accounted for via proportionally weighted penalties: larger constraints lead to more distinct differences in results when compared to a species-based approach where every conservation feature is given the same penalty factor. Nonetheless, with increasing pressure on conservation efforts, understanding what may or may not be captured within one metric will be important to guiding stakeholders.

This work serves as a case study in the rapidly expanding field of evolutionary-informed conservation biology, as well as identifying priority areas for the conservation of primate evolutionary history. With PD becoming a more commonly used metric in spatial conservation planning exercises (see Chapter 2), planners need to be aware of the spatial differences between PD-based plans compared to those that focus on species richness. Moreover, it is important to know how this difference can be influenced by the amount a plan is constrained by available area, particularly if PD is incorporated though an approach that accounts for the varying degrees of importance of conservation features by weighted penalties. This case study shows that, for primates, there is the potential for species richness to act as a surrogate for PD, but this comes with the understanding that important parts of PD may be excluded from priority areas. Including other evolutionary measures, such as evolutionary distinctiveness would help to elucidate such potentially important parts of PD. This chapter also presents a new approach to weighted branch-based spatial conservation planning (see Appendix I.) and II.) for the relevant R code) that provides planners with an alternative option to this new weighted branch-based approach. For example, with the conceptually novel idea of setting coverage targets for the internal branches of a phylogeny, planners may find it useful to be able to visualise these ranges in a GIS-based setting, all facilitated by the approach presented in this chapter, rather than creating the required MARXAN input files by summing matrices.

CHAPTER 4 OPTIMISING THE SELECTION OF SPECIES TO MAXIMISE PHYLOGENETIC DIVERSITY PROVIDES A NEW APPROACH FOR PHYLOGENETICALLY-INFORMED SPATIAL CONSERVATION PLANNING

4.1 INTRODUCTION

The current global biodiversity crisis is well documented (Ceballos et al. 2015; Hoffmann et al. 2010; Pimm et al. 2014). This crisis underpins current conservation efforts and is pushing the field of conservation biology to find new and more effective approaches to conserve biodiversity. It has long been argued that conservation decisions based purely on species richness are lacking as they do not take into account evolutionary history, and are therefore likely to underrepresent biodiversity (Crozier, 1992; Faith, 2002, 1992; Forest et al., 2007; Gumbs et al., 2020; Isaac et al., 2007; Rosauer et al., 2017). Approaches that account for evolutionary history suppose that when there is an ‘agony of choice’ (Vane-Wright et al., 1991) for conservationists operating in a world with limited resources, precedence should be given to the species that are the most distinct evolutionarily, *i.e.* species are not equal, the amount of evolutionary history they represent varies widely, and as such they should be not treated equally (Isaac et al., 2007).

Based on these arguments, the explicit inclusion of evolutionary considerations into conservation planning is now widely considered to be an important part of biodiversity conservation (Brum et al., 2017; Carta et al., 2019; Isaac et al., 2007; Olivieri et al., 2016). Phylogenetic diversity (PD) is increasingly being recognised as one such metric that is important to consider for the conservation of biodiversity (Faith 2008; Gumbs et al. 2020; Isaac et al. 2007; Tucker et al. 2019; see also Chapter 2). PD measures the amount evolutionary history represented by a species or set of species, and is calculated as the sum of the phylogenetic branch lengths (usually measuring the amount of evolutionary history in temporal units) that span a particular species or set of species (Faith, 1992). Studies have found that increased PD is associated with increased productivity (Cadotte, 2013; Coelho de Souza et al., 2019), as well as increased ecosystem stability (Cadotte et al., 2012). PD may also act as a surrogate for other important facets or biodiversity, such as functional diversity (Owen et al., 2019; Scherson and Faith, 2018) although the extent to which this is the case is disputed (Mazel et al., 2018; Wicke et al., 2020). In addition to these considerations, greater levels of PD provide added ‘option value’ for species, the so called ‘safety net’ for biodiversity to respond to changing conditions (Faith 1992). The growing recognition of the importance of PD for biodiversity conservation is reflected in the International Union for Conservation of Nature's (IUCN) decision to set up a PD taskforce designed to provide conservation practitioners with technical guidance to increase the protection of PD on a global scale (https://www.pdtf.org/).

The wider importance of PD to conservation is discussed in more detail in Chapter 1 and Chapter 2. The focus of this chapter is to introduce a novel approach for the inclusion of PD into spatial conservation through the optimal selection of species. Conservation approaches that focus on capturing PD are based around the fact that species do not represent equal amounts of evolutionary history, and so the extinction of one species or set of species may result in a greater loss of evolutionary history than extinction of another (Isaac et al., 2007). In a time-scaled phylogeny (for example, a phylogeny produced from a molecular clock analysis), this difference can be observed by comparing the sums of the branch lengths of different species or sets of species, which represent different amounts of evolutionary history. A PD-based approach to conservation planning aims to maximise the conservation of evolutionary history and so will favour species (or sets of species) that comprise longer branches (= more evolutionary history).

The emphasis on identifying and protecting the varying levels of evolutionary history represented by different species has led to an uptake in, as referred to in this thesis, weighted branch-based methods of conserving PD (see Chapter 2). Many of these methodologies use spatial prioritisation tools (*e.g.* MARXAN and Zonation), and decompose phylogenies into their constituent elements (branches [including internal branches]), and use these as individual conservation features, the spatial range of which is calculated as the cumulative range of the species at the descendant tips (Asmyhr et al., 2014; Carta et al., 2019; Pollock et al., 2015, 2017; Rosauer et al., 2017). A weighted branch-based approach using MARXAN allows for individual conservation targets to be set for internal branches of a phylogeny allowing for optimised PD-led conservation solutions to be identified (Asmyhr et al., 2014; Rosauer et al., 2017); optimised in the sense that they allow planners to capture targeted elements of a particular clade, as opposed to focussing on hotspots that may result in long branches being missed or underrepresented due to a lack of overlap in their spatial range (Veach et al., 2017).

Weighted branch-based approaches have the advantage of using an easily interpreted metric, branch length, which usually represents evolutionary time. However, there are several flaws with a weighted branch-based approach when using MARXAN to identify priority areas. One of these is related to the same reason why a weighted branch-based approach is powerful: the weighted target setting of internal branches. MARXAN accounts for these weightings via a penalty factor, and thus for the weightings to have an impact, some targets must be missed as it is only then that the penalties are taken into account by MARXAN, which attempts to minimise the total cost of those penalties. If all coverage targets are met, then by definition all internal branches meet their targets as well, without MARXAN having to acknowledge the penalties. In such a situation, PD is captured passively, without being considered explicitly.

MARXAN is designed to solve the minimum set problem, whereby the objective is to minimise the resources expended, subject to the constraint that all features must meet their conservation targets (Ball and Possingham, 2000). However, to place constraints on the amount of land available, via the ‘cost-threshold’ function in MARXAN as in a weighted branch-based approach, changes the problem to a maximum coverage problem, whereby the object is to maximise protection of features subject to the constraint that the resources used do not exceed a fixed and predetermined cost (Ball and Possingham, 2000). Although MARXAN can approximate the maximum coverage problem using its cost threshold function, as in Chapter 3 (also Carta et al. 2019; Rosauer et al. 2017), the results will likely be sub-optimal (Ball and Possingham, 2000). It would therefore be useful to not have to rely on the setting of a ‘cost threshold’ within MARXAN to constrain planning exercises, to ensure PD is always explicitly considered.

This chapter introduces a novel method for the inclusion of PD in spatial conservation. The approach optimises the selection of species for PD, prior to the use of a spatial optimisation tool, using the greedy algorithm in Phylogenetic Diversity Analyzer (PDA) (Chernomor et al., 2015). These species, once optimally selected to maximise PD, are then used as conservation features in a MARXAN planning exercise to identify priority areas for the conservation of PD. MARXAN is one of the most widely used spatial conservation tools in the world for the identification of protected area networks (Ball et al., 2009); thus, having approaches that utilise MARXAN for the effective protection of PD is likely to be important for the future of biodiversity conservation planning.

Another reason for developing an explicitly species-based approach to maximising the conservation of PD, rather than a weighted branch-based one, is that species are more tangible and arguably easier to base a conservation plan around and present to a stakeholder, compared to internal branches of phylogenetic trees that do not actually exist as "real” conservation features. Despite wide acknowledgment for the potential value of evolutionary history in the scientific literature (*e.g.* Cadotte et al. 2012; Faith 2019; Forest et al. 2007; Gumbs et al. 2020; Isaac et al. 2007; Jetz et al. 2014; Tucker et al. 2012) its application within new or existing conservation actions remains rare (Tucker et al., 2019). The EDGE (Evolutionarily Distinct and Globally Endangered) of Existence programme by the Zoological Society of London (ZSL) is an exception to this, but much of this work is still waiting to be used in real–world applications (Tucker et al., 2019). Numerous, potentially confusing metrics have been cited as a potential stumbling blocks to PD’s lack of uptake (Winter et al., 2013) and attempts have been made to clarify the use of these metrics (Scherson and Faith, 2018; Tucker et al., 2012). Development of a new conceptual approach for incorporating PD in conservation that utilises a unit of biodiversity that has a been widely employed in conservation, namely species, should (it is hoped) facilitate greater uptake of PD-based conservation by decision makers.

Utilising the novel method introduced in this chapter for the identification of priority areas for the conservation of PD, intervals of PD are explored in 10% increments, from 10-100% of the PD, for three orders of placental mammals: Artiodactyla (“odd-toed ungulates”, such as antelope, gazelle, and deer), Carnivora (mainly carnivorous mammals, such as foxes, weasels and cats), and Primates (such as lemurs, bushbabies, tarsier, monkeys and apes). These orders were chosen for the availability of the two key data elements of this study, namely comprehensive phylogenetic information (Upham et al., 2019) and range data (IUCN, 2019). As well as presenting a novel approach to PD-based spatial conservation planning, this chapter also investigates the possibility of optimising the amount of PD to target in a conservation plan, to give stakeholders a better idea of if and when disproportionate gains in biodiversity may be had for relatively little extra area. Trends within and between the three orders, in regard to the relationship between PD and the amount of area required to protect it, were also investigated.

During the main analysis for this chapter an unexpected result was found, namely that the relationship between the amount of PD captured by optimally selected species was almost identical across all three orders; this was investigated further by looking at the distribution of branch lengths making up the phylogeny of each order.

4.2 METHODS

4.2.1 DATA

An expert range map for all terrestrial mammals was extracted from the International Union for the Conservation of Nature's (IUCN) Red List online database (IUCN, 2019). This range map contains the known ranges and taxonomic information for species comprehensively assessed by the IUCN (IUCN, 2019). The data was downloaded as a shapefile into arcMAP (version 10.3) GIS software. From this shapefile, the global range maps for terrestrial species of the three orders under consideration, namely Artiodactyla, Carnivora, and Primates, were extracted as separate shapefiles.

The DNA-only species-level phylogeny for all extant mammals of Upham et al. (2019) was downloaded from http://vertlife.org/phylosubsets; this phylogeny includes 4098 species. This phylogeny was then modified to produce separate species-level phylogenies for Artiodactyla, Carnivora, and Primates. R (version 3.6.1) was used to prune out the three orders, producing a separate phylogeny for each order. The range data was then modified to retain only the ranges of the species present in these three phylogenies; any species that did not have range and phylogenetic data were excluded. After this taxonomic alignment, which also included inspection and correction for spelling incongruences, spatial and phylogenetic data remined for 209 artiodactyl species, 214 carnivoran species, and 295 primate species.

4.2.2 GRIDDING AND MARXAN DATABASES/INPUT FILES

A single planning extent was used, *i.e.* the same planning area, covering the entire range of all species in all three orders. The same basic approach used in Chapter 3 was used here to set up the planning extent. An equal area grid was created over the planning extent using the 'fishnet' tool in arcMap. The grid and maps were projected within arcMap to allow for area to be accurately calculated. A Behrmann projection was used as it is a global projection that also maintains correct relative area (directions are somewhat distorted in this projection but that is less important here compared to maintaining accurate relative area). The grid cells, or planning units as they are referred to from hereon and is standard terminology within spatial conservation planning suing MARXAN (Ball and Possingham, 2000) , were 110km^2 (~1 degree at the equator), which is a commonly used unit size for global conservation planning studies (*e.g.* Brum et al., 2017; Rosauer et al., 2017)). The grid comprised of 13,558 individual planning units and was clipped to the exact planning extent. Therefore, any units that occurred across the coastline were clipped to that perimeter and resulted in an area less than 110km^2, resulting in a more accurate account of species ranges when compared to approaches that do not account for exact planning extents (*e.g.* Brum et al., 2017; Rosauer et al., 2017).

Spatial planning analyses for each order were carried out independently of each other using MARXAN version 2.4.3 (Ball et al., 2009). The same planning unit file was used for all three orders and was created directly from the grid described above. The planning unit versus species file, which contains the information about how much of each species range is contained within each planning unit (Ardron et al., 2010), was created using the 'tabulate intersection' tool in arcMap. This was done individually for each order. Finally, the species file, which contains the target information for how much of each species to conserve, was created for each order. The species file contains three columns of information: species ID, target coverage value (the proportion of each species' range was used here as opposed to a raw figure), and species penalty factor (the penalty applied for missing targets). 17% coverage was chosen as it reflects the Convention of Biological Diversity's (CBD) 2020 Aichi targets, in which it stated as an aim in 2012 to have at least 17% of terrestrial areas conserved through protected areas by 2020 (Strategic Plan for Biodiversity 2011-2020. Aichi Biodiversity Targets; https://www.cbd.int/sp/targets/).

Base species files were created for the orders where the targets for all species were set equally, namely 17% of their total range as described above. Base files like this are not standard in a MARXAN analysis and have been employed here to allow for the processing of multiple sets of species. A base species file, where all the conservation features in question are set equally, can be then be used to create multiple bespoke species files. It can be thought of as a file where all the species are 'turned on' (set to 17% target coverage), and that can then be altered through the automated comparison to a subsetted list of species; the species not in the subsetted list are turned off and the resultant species target file is saved, before repeating the process with the next subset of species (see Appendix III.) for R code). The use of base files is explained further in the 'Running MARXAN' section below.

4.2.3 USING PHYLOGENETIC DIVERSITY ANALYZER (PDA)

Phylogenetic Diversity Analyzer (PDA) (Chernomor et al. 2015) is a software tool that allows the user to compute and maximise species richness, PD, and split diversity for a given phylogenetic tree input file (which can be in either Nexus or Newick format). Here, PDA was used to optimise selection of species to maximise PD. PDA is command line driven, run here in Windows 10 using version 1.0.3 of PDA. PDA produces a *.pda* file which contains a list, or set of lists, of optimally selected species, optimally selected to maximise PD, for a user defined number of species.

For a given phylogeny, PDA can calculate the optimal set (that is to say, the smallest number) of species that represent a given amount of PD; for example, the smallest number of species that represents 90% of the PD for a given phylogeny. In general, this set of species is likely to contain species with long branches that are not closely related to each other, as such combinations of species will have higher levels of PD. The levels of PD that were investigated here ranged from 10%-100% at 10% intervals (±0.5%, as the phylogenies could not always be perfectly decomposed into the exact amount of PD required).

When trying to calculate optimal sets of species for differing levels of PD, the user must first determine a specific number of species (the 'K value'), and PDA will compute the set of species that equates to the maximum amount PD for that number of species. Depending on how many decimal places the branch lengths are calculated to (which will influence how many branches have exactly the same length), and how big the tree is (larger trees are more likely to have more branches with the same length), it is likely that different combinations or sets of species (referred from here as 'sets') will equate to the same amount of PD. This was indeed the case here (see Table 4.1), and so all sets representing the same defined PD value were analysed separately. This element of the approach provides a planner with flexibility, as they can use other factors to select from these sets of species that have already been optimised to maximise PD. Here, the set that led to the MARXAN solution (17% target for included species) with the smallest total area was chosen as optimal. However, it is possible to incorporate other important factors such as rarity or threat level, which is explored further in the discussion.

4.2.4 RUNNING MARXAN

Within the MARXAN databases for each of the three orders, there is an input file that contains the planning unit file, the planning unit versus species file, and the base species file where all species targets are set to 17%. Using the optimal sets calculated by PDA, MARXAN was then run for each combination of species, at each interval of PD, from 10%-100%. As noted above, in many cases, the same amount of PD was represented by multiple different sets of species, in some cases well over 100 different sets (see Table 4.1). Given the number of sets across all values of PD, 10-100%, (682 for Artiodactyla alone) it was necessary to develop an approach for automating the MARXAN portion of the analysis. For this, R (version 3.6.1) was used. For each order, the *.pda* files (which contain the sets of species for a given amount of PD) were used to automate the creation of bespoke species files for every set. This was achieved by using the *.pda* files in conjunction with the base species file, which contain all the species for that order. Any species that did not appear in the list of species in the *.pda* file for a given amount of PD had its species target set to 0 in the base file, leaving the remaining species at a target coverage level of 17%. This resulted in a different species target file for each set; for example, 682 species target files in the case of Artiodactyla, representing all sets for a given value of PD (see Appendix III.) for R code).

Using R to automate the process (see Appendix IV.) for R code), MARXAN was run for each target file, for each set, at each amount of PD separately for each order's database. MARXAN was run 200 times (as per the MARXAN good practice handbook (Ardron et al., 2010)) for each set, with an annealing control of 100,000 iterations (MARXAN's default setting). MARXAN minimises "cost" as part of its objective function, optimising solutions to meet targets at lowest possible cost. Cost can be based on a variety of different criteria, but here it was set as equal to area (common practice when no real-world cost data is used (Ardron et al., 2010), which was measured in km^2. Thus, in this study, MARXAN was selecting the combination of planning units that would contain at least 17% of the range of the species within a given set, whilst requiring the least possible area. The species penalty factor (SPF) was optimised based on the results of preliminary analyses, which found that an SPF of 1000 consistently allowed MARXAN to meet all its targets ~96% ± 2% of the time, both between and within orders. This is important as it is imperative to balance the objective function at MARXAN's core, and having an SPF that meets targets at this level, close to but not 100%, ensures that the SPF is not set too high which would restrict MARXAN's performance but also not so low that the targets set are not achieved often. For example, in a scenario where the SPFs are set too low, the 'lowest cost' solution (which is what MARXAN is trying to find) may not achieve multiple targets as the penalties are not set high enough for MARXAN to ensure they are selected; this is because the cost of adding additional planning units is more than the small penalties incurred by missing targets. Conversely, if the SPFs are set very high, then the simulated annealing algorithm will only be able to explore a limited number of possible solutions (Ardron et al., 2010).

4.2.5 SET SELECTION

The outputs from the running MARXAN are MARXAN solutions for every set of species, at every interval of PD (from 10% to 100%). It is important therefore, when employing this approach, to decide how to identify which set of species represents the optimal set to conserve at each PD interval. It could be the set that contains the most or the least endangered species, for example, but in this case area was used to identify the optimal set of species for each PD interval *i.e.* the set of species which could be protected at 17% of their range in the least amount of area.

See Figure 4.1 for a full workflow of this new approach.

4.2.6 BINNING BRANCHES

In order to explore further the relationship between optimally selected species and the amount of PD they capture, the shape of each phylogeny was compared, specifically the distribution of proportionally different branch lengths. To do this, all branches (internal and terminal) of the phylogeny for each order were binned according to the percentage of the total root-to-tip length of the tree that branch represents. For this exploratory analysis, 5% bins were chosen as these seemed enough to fairly reflect the distribution of branch lengths without creating too much noise. The distribution of branch lengths in the three phylogenies were compared qualitatively.

Table 4.1 Number of sets of species, as identified by Phylogenetic Diversity Analyzer (PDA), that represent a given amount of phylogenetic diversity within each order of species. k = number of species at each phylogenetic diversity interval**.**

	Number of sets within each order		
Amount of phylogenetic diversity (+/-1%)	**Artiodactyla (209 species)**	**Carnivora (214 species)**	**Primates (295 species)**
10%	**2 (k=2)**	**1 (k=3)**	**1 (k=3)**
20%	**4 (k=4)**	**1 (k=8)**	**6 (k=9)**
30%	**16 (k=10)**	**1 (k=13)**	**24 (k=17)**
40%	**64 (k=18)**	**2 (k=20)**	**96 (k=28)**
50%	**109 (k=29)**	**12 (k=28)**	**107 (k=41)**
60%	**112 (k=43)**	**48 (k=40)**	**111 (k=60)**
70%	**119 (k=61)**	**96 (k=55)**	**117 (k=88)**
80%	**127 (k=86)**	**114 (k=77)**	**125 (k=128)**
90%	**128 (k=121)**	**120 (k=111)**	**128 (k=185)**
100%	**1 (k=209)**	**1 (k=214)**	**1 (k=295)**

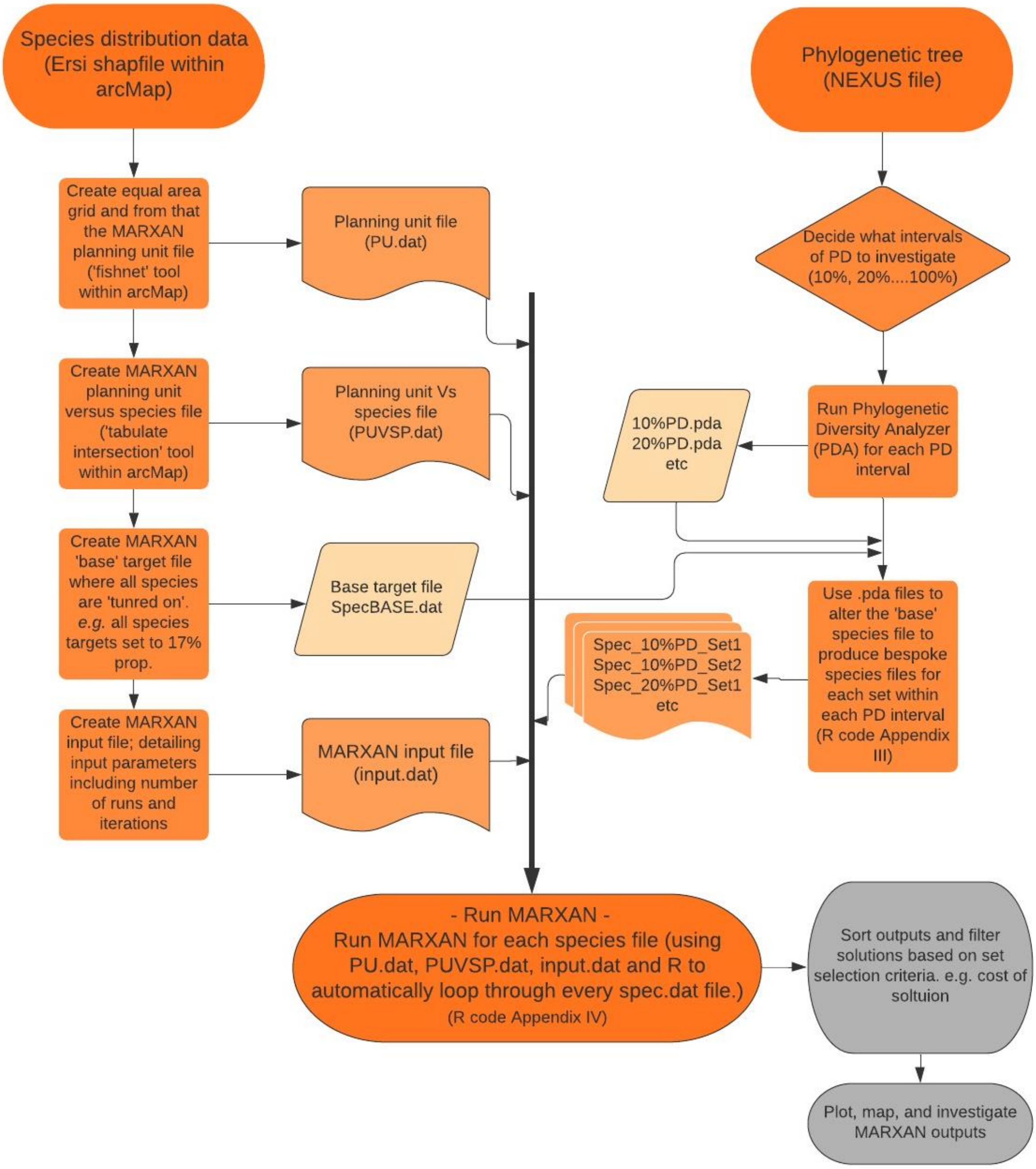

Figure 4.1 Workflow for a novel approach to incorporating phylogenetic diversity (PD) into spatial conservation planning. Process utilises GIS, MARXAN, and R. Including R code Appendix III.) and IV.)

4.3 RESULTS

As shown in Figure 4.2, the relationship between PD and the area required to protect it is broadly linear. There are some similarities in the relationship between PD and area between the orders. For example, the steepest increases are found between 30-70% PD in all three orders. The interval that is associated with the largest increase in area is found within Primates from 40% to 50% PD. This 10% increase in PD costs ~24% of the total area needed to conserve 100% of Primate PD. This maximum increase is also found within this middle portion of PD (30-70%) for the other two orders; with Artiodactyla requiring an increase of ~21% to raise PD protection from 60%-70%, and Carnivora experiencing its most expensive increase from 30%-40%, costing ~18%.

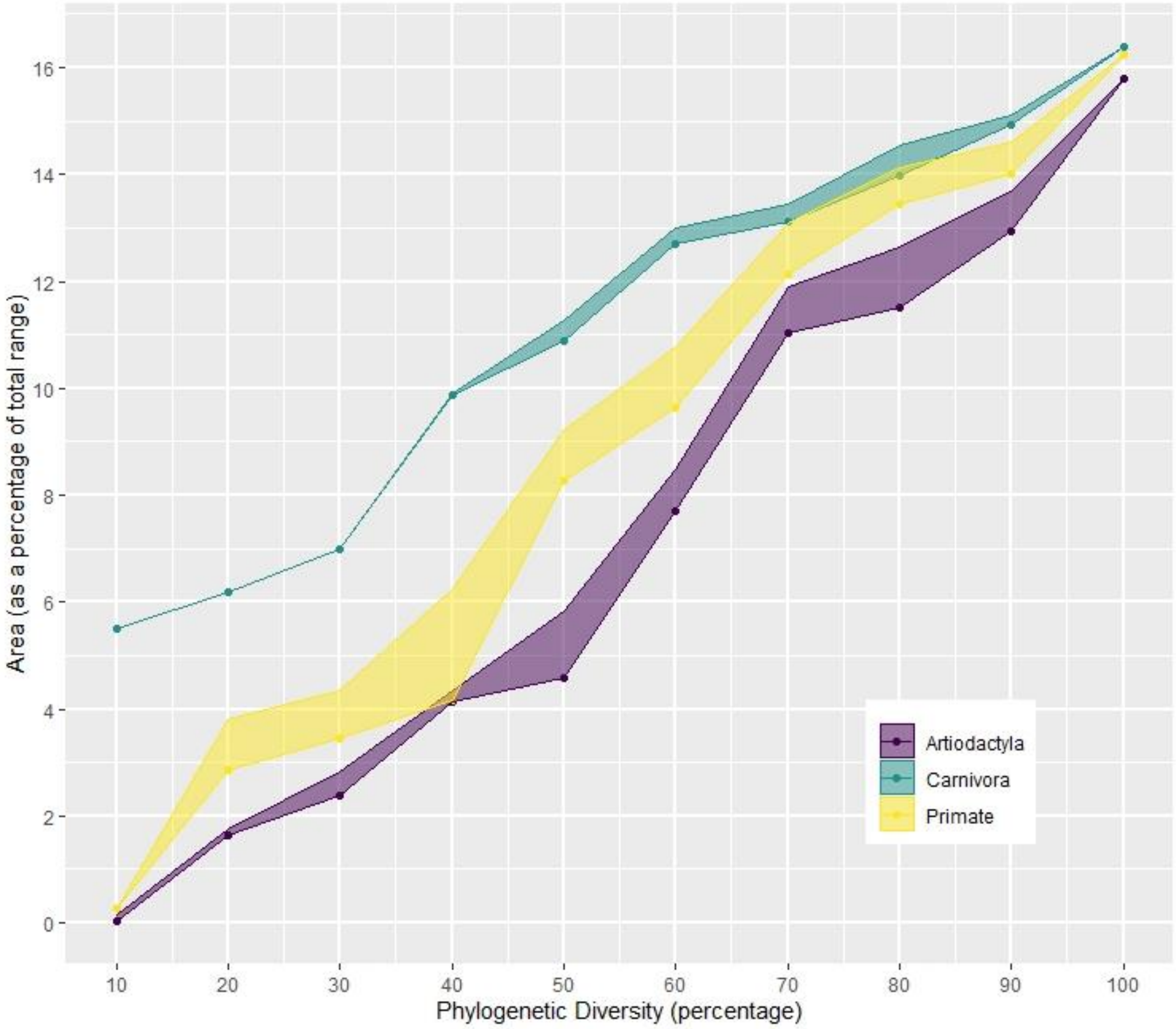

Figure 4.2 The area required to protect different percentages (10-100% in 10% increments) of total Phylogenetic Diversity (PD) for the placental mammal orders Artiodactyla, Carnivora and Primates. Analyses were implemented using Phylogenetic Diversity Analyzer (PDA) and MARXAN. The lower part of the line, with the dots, represents the set of species that required the least amount of area for that order at that level of PD. The upper part of the line, without any dots, represents the set of species that requires the most area, for that PD interval. The shaded portion of the lines represents the variance in area amongst sets at each PD interval. Area is given as a percentage of the total area of the combined, non-overlapping, ranges of the species within each order; this allows for relative comparisons between orders.

This 'expensive' portion of phylogenetic diversity is also where we see the most disparity between the orders in the area/PD relationship. This disparity decreases markedly at 70% PD. This trend continues between 70% and 90% PD, with the smallest difference seen at 100% PD; all three orders, can be protected under this policy-driven 17% coverage target, within 0.69% total area of each other (Artiodactyla = 15.78%, Primate = 16.24%, Carnivora = 16.37%).

There is variation in the area required to meet conservation targets for the different sets of species within a given PD interval, which is represented in Figure 4.2 by the shaded portion of the lines. Primates experienced the highest variation: when protecting 40% of primate PD, the combination of optimally selected species results in a variation in cost of just over 2% of the total area available, which equates to ~12.5% of the cost of protecting 100% of primate PD. On the other hand, Carnivora has the smallest amount of set variation, in fact not having any until protecting PD at 50%. Carnivora peaks in set variation at 80%, where it is 0.56% of the total area required to protect 100% of its PD.

The differences seen between the three orders in Figure 4.2 may be explained by variations in species range size and the amount of range overlap. Figure 4.3 shows the variation in species range within each order. Carnivora have the largest median range (2.5% of the order’s total range), more than double that of Artiodactyla (0.7%) and Primates (0.3%). Carnivora also has the biggest variation in range size with a ~7% interquartile range, which is more than three times that of the other two orders.

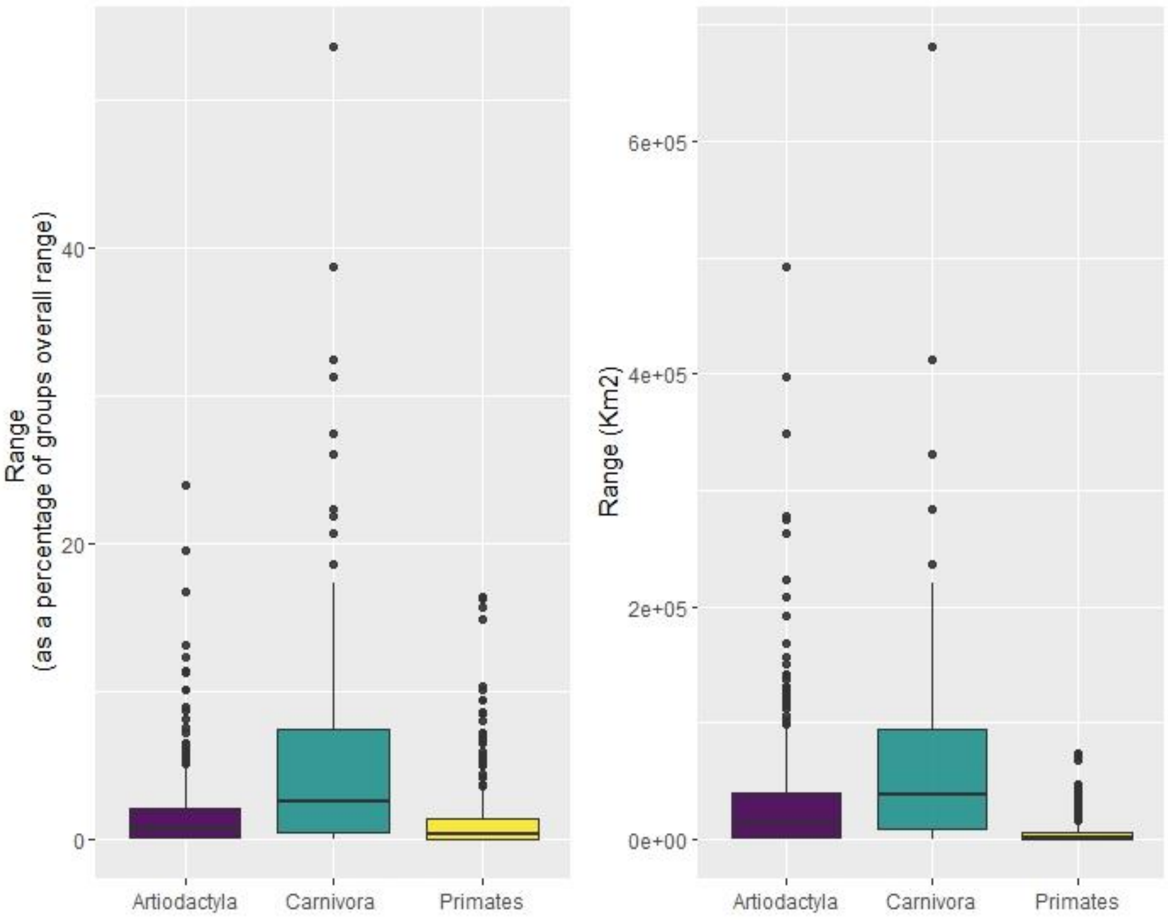

Figure 4.3 Boxplots for species range within each order. a.) shows the range as a percentage of the order's overall range and b.) shows the absolute values in Km^2. Boxplot presents 25th, 50th, and 75th percentile, with the whiskers showing the smallest and largest values within 1.5 times the interquartile range of the lower and upper quartile, and the outliers are >1.5 times and <3 times the interquartile range beyond either end of the box.

The amount of overlap in species ranges within each order has been approximated using species richness within a planning unit (Figure 4.4). While this does not represent the exact amount of range overlap that exists within an order, the manner in which MARXAN operates means that all species that occur within the same planning unit are considered overlapping, and by conserving a planning unit that contains a portion of a number of different species' ranges, all these species will be considered protected. The species richness boxplots follow a similar pattern to those for species range (Figure 4.3). Carnivora has the highest median species richness per planning unit as a percentage of the order's total range (5.6%) and the largest interquartile range (3.8%), with Artiodactyla and Primates far lower (Artiodactyla median species richness = 1.9%, and inter quartile range = 1.43%; Primates = 1.35% average species richness, and 1.7% inter quartile range).

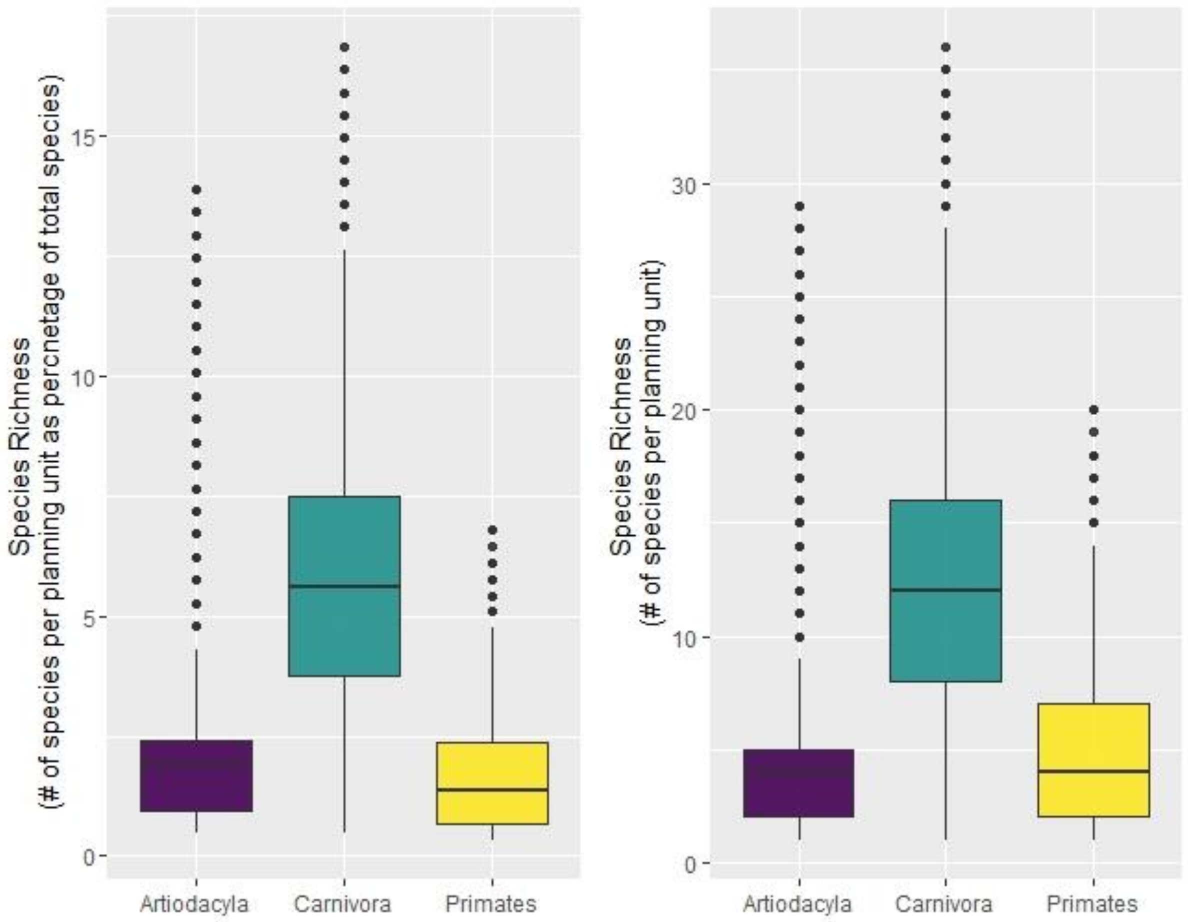

Figure 4.4 Boxplots for species richness within each order. Species richness was calculated as the number of species within a planning unit. a.) shows species richness as a percentage of the total number of species within the order and b.) is the absolute number of species. Box presents 25th, 50th, and 75th percentile with the whiskers showing the smallest and largest values within 1.5 times the interquartile range of the lower and upper quartile, and the outliers are >1.5 times and <3 times the interquartile range beyond either end of the box.

The relationship between the number of species (when selected in an optimised manner to maximise PD) and the amount of PD they represent is not linear (Figure 4.5). The proportion of PD captured by species, when they are selected in the optimal approach used here, increases in an approximately logarithmic fashion. This relationship is consistent amongst the three orders explored here (Figure 4.5).

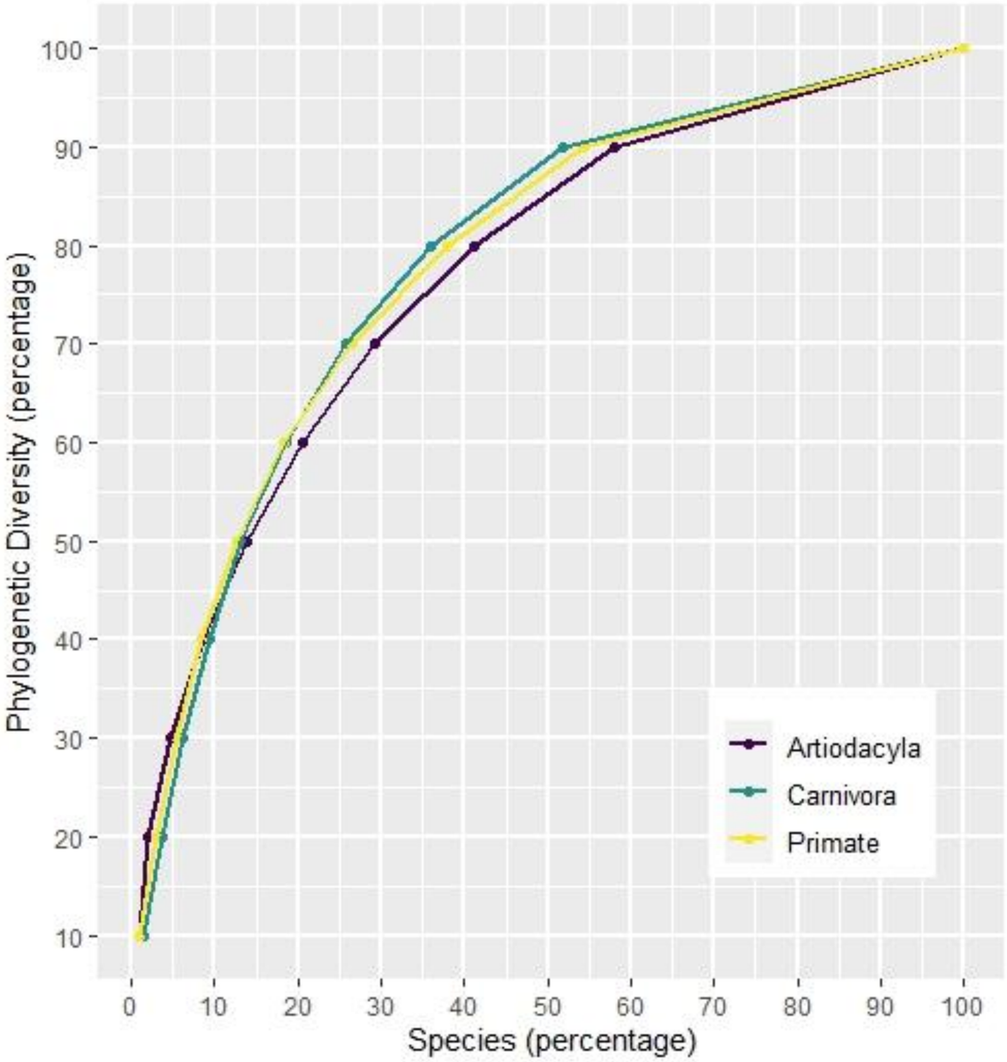

Figure 4.5 The amount of Phylogenetic Diversity (PD) captured by optimally selecting species for PD. Species are represented as a percentage of the total number of species for that order (Artiodactyla n=209; Carnivora n=214, Primates = n295).

The distribution of relative branch lengths within the phylogeny is very similar in all three orders (Figure 4.6). The clear majority (>67.5%) of branches are between 0-5% of the total root-to-tip length of the phylogeny in all three orders. The length of branches then decreases steadily to 45-50% total tree length. There are some notable outliers in the Artiodactyla, namely Camelidae and Hippopotamidae, both of which descend from internal branches that are longer than 80% of the total root-to-tip length of the phylogeny.

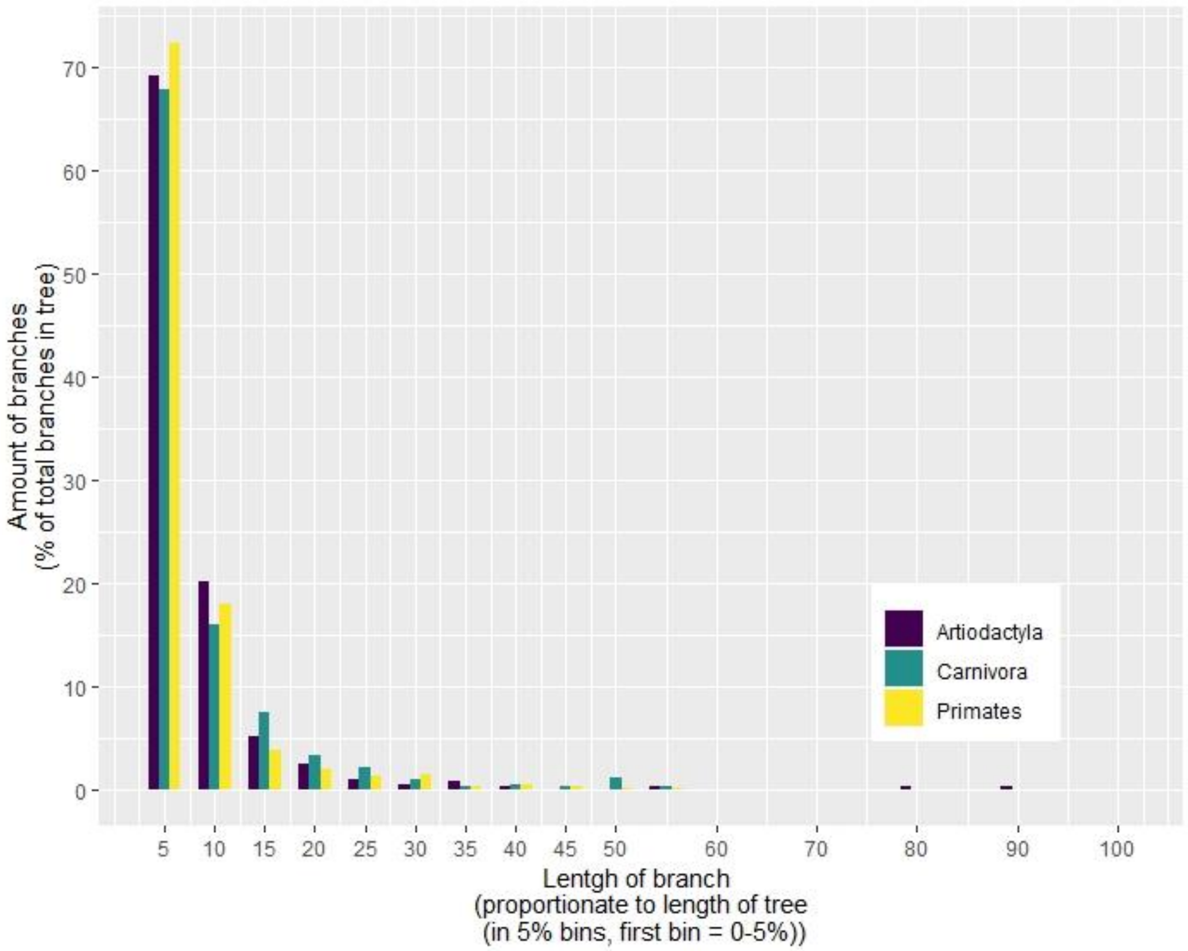

Figure 4.6 The composition of the phylogenetic trees for Artiodactyla, Carnivora, and Primates, broken down into the distribution of branch lengths, binned into 5% bins. Branch lengths were calculated proportionately to the total root-to-tip length of the phylogeny in question. The trees have been created through the modification of an initial tree from Upham et al. (2019) representing 4098 mammal species.

4.4 DISCUSSION

This work introduces and applies a new approach for incorporating PD into spatial conservation planning. This approach optimises conservation action by firstly optimising species selection based on PD, and then subsequently optimising spatial conservation (protected area design) for those species. This approach evolved out of the methodology used in Chapter 3. The approach in this chapter demonstrates how PD can be prioritised in space through the optimised selection of species, without the use of a hotspot approach that calculates PD scores for individual planning units (which may underrepresent important elements of a phylogeny *e.g.* Brum et al., 2017; Gumbs et al., 2020), or mapping internal branches of phylogenies as in a weighted branch-based approach (*e.g.* Chapter 3; Carta et al., 2019; Rosauer et al., 2017). This approach also analyses the relationship between species as a unit and PD, and how this can influence spatial conservation planning.

The results of the main analysis here show that the amount of PD included within a conservation area does not scale linearly with the size of the area. While this is perhaps unsurprising given the different factors at play, such as varying species range size and the degree of range overlap between species, this relationship has important ramifications for spatial conservation. Here, it is clear that there are large gains to be made in PD conservation that can be achieved for the addition of relatively small amounts of area. For example, it is possible to increase the amount of Artiodactyla PD that is protected, globally, from 70 to 80% for an increase of only 0.5% area. Conversely, increasing the amount of PD protected from 60 to 70% requires over six times the amount of area. Disparities like this can be observed across the spectrum of PD intervals for all three orders (Figure 4.2). These disparities exemplify the importance of considering the varying amounts of evolutionary history represented by different species. Understanding how the relationship between species and the PD that they represent scales allows for the optimisation of PD protection with limited resources, and allows for the identification of situations where disproportionately (as measured by the amount of area needed) large gains could be made in the protection of biodiversity. This gives planners and stakeholders the power to know when and where it is more worthwhile to push for extra area.

Using species optimisation and structured conservation planning, this study has shown that large gains in PD conservation can be made for small increases in the total area of conservation areas. There are few other studies (Pollock et al., 2015; Rosauer et al., 2017) that explore the relationship between PD and area in an optimised planning exercise in this way *i.e.* how each metric, PD and area, scale in relation to one another. Instead, most work in this field has focused on identifying PD hotspots (*e.g.* Daru et al., 2018; Brum et al., 2019; Carta et al., 2019). However, Pollock et al., (2015) and Rosauer et al., (2017) do present findings on the amount of PD that is captured within different proportions of particular study sites, optimised using prioritisation software (Zonation and MARXAN respectively). Both present similar results that show that large gains can be made for small increases in area. The relationship shown between PD and area in both of these studies is smooth, exponential or logarithmic in shape (depending on how they have presented their data); this relationship is similar to the relationship between PD and species presented in this chapter in Figure 4.5 with initial large gains in PD slowly decreasing to a plateau. Whilst Pollock et al.'s (2015) and Rosauer et al.'s (2017) findings are similar to those found here, with large PD gains being made for relatively little area at early PD intervals, the relationship found in those previous studies is markedly smoother and plateaus at higher levels of PD. In this chapter, however, the relationship does not plateau and there are still large potential gains in PD for relatively little extra area even at the upper PD intervals. The differences in the findings between Pollock et al., (2015) and Rosauer et al., (2017) and the work presented in this chapter are likely an artefact of different approaches, as opposed to the different data sets. This is particularly clear when comparing this chapter to Rosauer et al. (2017), who were also using a global mammal data set. Rosauer et al. (2017) and Pollock et al. (2015) both use a weighted branch-based approach to identify priority areas for the conservation of PD. Given the nested nature of internal branches, with internal branches inherently captured by the inclusion of branches closer to the tips, it would be expected that the relationship between the amount of PD captured by species would increase more smoothly (as in Figure 4.5) as area increases. The adoption of a weighted branch-based approach for the identification of priority areas for the conservation of PD may limit the ability of planners to take full advantage of the differing amounts of PD that different species represent when compared to an approach that optimises species selection.

The other study that presents results from a similar approach to the one presented in this chapter is Jetz et al., (2014). Their work incorporated rarity together with evolutionary distinctiveness (ED), a measure of how isolated a species is on its phylogenetic tree (Vane-Wright et al., 1991), to create a new metric - evolutionary distinctiveness rarity (EDR) - that they applied to threatened bird species. Birds were ranked initially by their ED score, and this was then weighted against the size of their range, with species that were both evolutionarily distinct and rare considered to be conservation priorities. As part of the study, Jetz et al., (2014) employed a similar strategy to the one employed here, namely using a greedy algorithm to prioritise species for PD, which they then used to compare against an ED-based planning approach. Their results in this part of their analysis, which did not make up part of their main findings, show a similar broadly linear relationship between the amount of PD conserved and the area required to do so, with plateaus, *i.e.* minimal gain, at extreme low and high PD intervals. Although Jetz et al. (2014) did not elaborate on this result, which was only a small component of their overall study, a comparison can be made to results presented in this chapter; the order that gave the most similar results to the bird species considered by Jetz et al. (2014), *i.e.* that had the smoothest relationship between PD and area, was Carnivora. Carnivorans, like the global bird species in Jetz et al. (2014), have a relatively large median average range size. Range size is something that was found to be an important element of the spatial approach used in this chapter.

An important aspect to consider within spatial conservation plans is the amount of overlap that exists between the range of species. The more overlap there is between species ranges, the smaller the amount of area needed to meet targets. Here, species richness per planning unit was used as a crude measure of overlap. Carnivora had the highest mean average of proportional species richness of the three orders (Figure 4.4), which implies that less total area would be needed to conserve species, compared to a clade with lower proportional species richness such as Artiodactyla, but this is would be offset by the (on average) large range sizes of Carnivora; nonetheless, if there was less overlap in species ranges, the total area needed for conservation would be far greater. However, this measure of overlap is extremely coarse and further investigation is required in order to draw more confident conclusions on the impact of overlapping ranges when employing the methodology presented here.

Species range and overlap are important elements of traditional spatial conservation, and the way they interact with the novel approach for incorporating PD that is presented in this chapter requires further discussion. The first stage of the approach presented here optimises exclusively for PD, unaffected by any spatial consideration. Thus, the species, or combination of species, that represent the most PD are included before those that are less phylogenetically distinct. Therefore, in this approach there will be sets, that represent the same amount of PD, but which contain species that are widely distributed, where the resultant MARXAN solution will require a lot of area compared to sets that contain more species with smaller ranges. This goes some way to explaining the variation in the amount of area required to protect different sets representing the same amount of PD within the three orders examined here: the more variation in range size and range overlap associated with varying levels of PD, the more variation in area required between sets. Further investigation is required explore the interaction between species range, overlapping ranges, and PD when using this new approach.

Artiodactyla, Carnivora, and Primates all require the same percentage of area (16% ±0.5% of the order's total range) to protect 100% of their PD. This may be an artefact of the approach, which targets of 17% of the total range of each species. However, in Rosauer et al. (2017) a similar result is found with 17% of land needed to capture 100% PD, and in their approach, targets were set to 25%. Rosauer et al. (2017) used data for all terrestrial mammals, and so includes species from all mammalian orders (not just the three considered here), so this similarity may be coincidental. The targets in this chapter were set at 17% to reflect the CBD's protected area targets. However, there is no clear evidence in the CBD rationale for 17% that the figure is anything more than a relatively arbitrary number, based more on perceived achievability than ecological significance (CBD https://www.cbd.int/sp/targets/rationale/target-11/); nonetheless, the wide acceptance of the CBD (with 196 signatory countries) 17% was deemed to be a suitable target to use here. In real-world scenarios it is likely that stakeholders would utilise the flexibility of MARXAN to set bespoke and carefully calculated coverage targets for each conservation feature, dependant on the ecological requirements for protection and the aims of the conservation area; however, in the context of this study, and others like it, such targets would make direct comparisons between scenarios difficult to make, therefore a uniform target was used with calibrated species penalty factors allowing for comparisons between scenarios to be made. Studies that have explored the differences in spatial prioritisation outputs for the conservation of PD between different taxonomic orders often focus on large taxonomic groups, *e.g.* all mammal species globally (Brum et al., 2017; Rosauer et al., 2017). Working with such large groups may result in important insights being obscured, for example the impact that differences in species range can have, something that may explain the different results between the three mammalian orders considered here. However, clade-specific differences may be found at all taxonomic levels; for example, within Primates it would not be unsurprising to find differences in the spatial plans for great apes (Hominidae) compared to Old World monkeys (Cercopithecidae). Nevertheless, as researchers continue to search for 'one size fits all' type conservation recommendations, it is important to keep in mind the substantial differences that may exist within and between cases, as exemplified by the results in this chapter when looking at how the different orders behaved in regard to the relationship between PD and the amount of area required to conserve it (see Figure 4.2). One of the major advantages of this novel approach, for the identification of priority areas for the conservation of PD, presented here is the ease with which other metrics, such as rarity or threat level, can be integrated as well as the fact it avoids the use of the cost threshold option; the use of the cost threshold can result in sub-optimal results if not used extremely carefully (Ardron et al., 2010). The ability to integrate other metrics is a consequence of the approach having two stages, the first of which, the greedy optimisation of species for PD, does not consider the spatial extent of species at all, and therefore often results in multiple different sets of species representing the same amount of PD. It is the identification of these different sets, which gives conservation planners a choice of different options, that allows for the integration of other useful metrics. In this chapter area was used, but functional diversity, rarity (*e.g.* Jetz et al., 2014), or a combination of these or other metrics, could just as easily be integrated into the analysis, providing more options for planners and stakeholders.

The proportion of species within in each order that was required to represent increasing amounts of PD further highlights the fact that all species are not equal in the amount of evolutionary history they represent (Figure 4.5). It is optimising this variation in the amount of PD different species represent, demonstrated in Figure 4.5, that forms the basis for the approach presented in this chapter. With ~80% of PD being represented by ~40% of the species across all three orders, and evidence in the literature showing that when species are chosen randomly the relationship between species and the amount of PD they represent is approximately linear (Jetz et al., 2014), the benefits of incorporating this knowledge, on the varying amount of PD represented by species, into a spatial conservation plan are substantial. This is even more pertinent given that resources are almost always limited, meaning that planners and stakeholders are looking to gain the most out of minimal land use (McCarthy et al., 2012).

An unexpected outcome of calculating the relationship between optimised species versus PD (Figure 4.5) for Artiodactyla, Carnivora, and Primates was the similarity between the three orders: all three have almost identical curves. Although this logarithmic curve was expected, as a greedy algorithm was used to select species to maximise PD, the very close similarity in the shapes of the curves for the three orders was not, raising the possibility of the existence of some underling common cause (either biological or analytical). One possibility is that the similarities are due to the way the three phylogenies are structured: specifically, if all three orders had a similar distribution of branch lengths (*i.e.* a similar proportion of “short”, “medium” and “long” branches), then a greedy approach to selecting species for PD would result in similar outputs. Indeed, this does appear to be a likely explanation for this phenomenon: the phylogenies of each of the three orders have similar distributions of relative branch lengths (Figure 4.6). This was an unforeseen, perhaps surprising finding and one that requires further investigation. However, it further highlights the need to consider species as more than equivalent units, and that when this is done, a greater proportion of biodiversity can be protected.

There are limitations to the analysis here, most notably in the lack of actual cost data. In a real-world planning scenario, the cost of protecting land is unlikely to be constant, with other factors such as land use, management status, and human pressure (Bowler et al., 2020) having an influence (Ardron et al., 2010). However, the aim of this chapter was to introduce a new methodological approach while exploring trends in and amongst species and PD, and for that the widely accepted use of area as a surrogate for cost, which works under the assumption that bigger areas are more costly to conserve and are therefore less likely to be realised, was appropriate (Ardron et al., 2010). Another limitation is the use of proportional targets for species. While this allowed for easier comparisons to be made between and within taxonomic groups (in this case, mammalian orders), it does not take into account the varying levels or protection that might be required for species, particularly those that have very small or very large ranges, where protecting 17% of their range may not be adequate to maintain the population. Proportional target setting also means careful consideration is needed when making comparisons between orders; the large variation between the average range size of the species within each order results in substantial differences in the area demand between the orders given that proportional targets have been used. Substantial differences in area demand make direct comparisons across orders difficult; however, for the purpose of this work it provided a useful exploration of the application of a new methodology for the conservation of PD across multiple orders.

The two-stage, species-based, phylogenetically-driven spatially optimised approach introduced in this study provides many advantages of capturing PD. As discussed in the introduction 4.1, this approach allows planners to reframe the conservation of PD around species ranges, which are more broadly utilised within spatial conservation compared to phylogenetic branches or PD scores; this is done without the drawbacks of simply using species richness, which fails to capture evolutionary history and may result in underrepresentation of evolutionarily distinct species. Further to this, future works should extend this approach by trying to incorporate other key metrics such as threat level and rarity, as well as human pressure (Gumbs et al., 2020; Jetz et al., 2014). Spatial sale is something that also needs more attention in the field of PD-based conservation, specifically whether the findings of such large-scale studies, which is the theme in the literature and in this chapter (*e.g.* Brum et al., 2017; Gumbs et al., 2020; Quan et al., 2018; Rosauer et al., 2017; Simkins et al., 2019) translate to more local case studies.

This chapter presents a novel approach to the inclusion of PD into spatial conservation. While the underlying principle of PD-informed conservation is that all species are not equal, species themselves are still a widely utilised and understood conservation feature, something that is likely to continue for the foreseeable future. It is therefore hoped that the new species-based, PD-driven approach presented here will facilitate the wider use of PD as a metric to inform conservation choices made by planners and stakeholders, as part of the growing movement for more evolutionarily informed conservation.

CHAPTER 5 “SPLITTING” VS "LUMPING" AND PHYLOGENETIC DIVERSITY: THE IMPACT OF TAXONOMIC CHANGES ON THE SPATIAL CONSERVATION OF EVOLUTIONARY HISTORY

5.1 INTRODUCTION

Taxonomy provides the basis for measuring biodiversity; it provides a system of naming and classifying organisms that is used not only in the study of biodiversity but across the whole of biology (Agapow et al., 2004; Mace, 2004; Thomson et al., 2018). Taxonomy is therefore at the core of conservation biology, which aims to conserve biodiversity. Species-level taxonomy is of particular importance, because species are usually the basis of conservation prioritisations, with species richness being a key metric in many studies and plans (Allan et al., 2019; Myers et al., 2000). Species are also central to international conservation organisations such as the International Union for Conservation of Nature (IUCN), who provide globally recognised conservation assessments of species via their Red List (https://www.iucnredlist.org/).

Phylogenetic diversity (PD) is an increasingly important metric in spatial conservation (Gumbs et al., 2020; Isaac et al., 2007). In approaches that attempt to maximise the conservation of PD, such as those presented in Chapter 3 and Chapter 4, an understanding of which evolutionary lineages should be considered as separate species is key to calculating PD, as this metric is usually calculated based on species-level phylogenies. However, there remains an ongoing debate within biology on exactly what a species is, and how species should be recognised (Agapow et al., 2004; Gippoliti, 2019; Heller et al., 2013; Zachos et al., 2013). Although PD-based approaches to conservation planning have been argued to overcome the shortcomings of species-based methods (Rosauer et al., 2017), the former will still be impacted by the use of different species concepts, because this will affect how many species are present in the phylogeny that is used to calculate PD. Thus, understanding the debate around species concepts, and the impact different concepts are likely to have on PD-based approaches to conservation planning is important to the continued uptake of such approaches. Nevertheless, this issue remains understudied.

There continues to be a debate within the literature about exactly what species are (what species concept to use), and how they can be accurately identified (what species criteria to use) (Christenhusz, 2020; Garnett et al., 2020; McClure et al., 2020; Wilkins, 2009). Recent estimates indicate at least 34 different species concepts (Zachos, 2018). It is unlikely that a general consensus will be reached regarding this issue in the near future (Zachos, 2016), and it is not the aim of this work to resolve this issue; no judgement is made here regarding whether one or more species concepts is “better” than others. Instead, it tests for the first time what the impact of the two most commonly used species concepts - namely the Biological and Phylogenetic Species Concepts - has on optimised spatial conservation planning using the African members of the mammalian family Bovidae (which includes animals such as antelope, gazelle, duikers and wildebeest) as a test case.

The Phylogenetic Species Concept (PSC) defines a species as the smallest population-level group of organisms that is diagnosably distinct from other such groups (*e.g.* Cracraft, 1983; Groves, 2001), and is more likely to “split” species (Zachos, 2018). The main alternative to the PSC is the Biological Species Concept (BSC), where species are defined as groups of actually (or potentially) interbreeding organisms which produce fertile hybrids (Mayr, 1943), and it is more likely to “lump” species when compared to the PSC. The debate around these two schools of thought is extensive and at times heated (*e.g.* Gippoliti, 2019; Gippoliti et al., 2013; Gippoliti and Groves, 2013; Groves, 2013; Zachos, 2019, 2015; Zachos and Lovari, 2013), with proponents of the PSC accused of ‘taxonomic inflation’ by those who favour the BSC (Isaac et al., 2004), whereas proponents of the BSC have been accused of ‘taxonomic inertia’ by those who favour the PSC (Gippoliti et al., 2018). Both sides argue that the opposing view has, amongst other issues, detrimental impacts on conservation biology. Both “splitting” and “lumping” have been cited as having the potential to inhibit the protection of species (Gippoliti et al., 2018; Zachos, 2015). In the case of “splitting” (as typically occurs under the PSC), it has been argued that the cohesive protection of species is diluted by subdividing one species into many species, each of which now requires conservation assessment, and which are usually spatially disjunct and often have very small ranges (Zachos, 2015). In the case of “lumping” (as typically occurs under the BSC), what is supposedly a single species may actually be made up of multiple distinct species, which may have differing endangerment levels and conservation needs (Gippoliti and Groves, 2013).

Despite this often heated debate within the structured community, few studies have tried to empirically investigate the impact of taxonomic changes on the conservation of biodiversity (Simkins et al., 2019). Morrison et al. (2009) reviewed the literature for cases of where the protection of threatened or endangered species or populations had changed due to taxonomic revisions, and found no consistent impact of a taxonomic change leading to changes in the level of conservation in regard to funding or efforts towards monitoring and research of a species or clade. However, Morrison et al.'s (2009) review was limited by its qualitative nature, it incorporated only 20 different species-level examples from across multiple clades, and it considered many different countries with a variety of different conservation laws and systems. Nonetheless, their study was the first to assess the impact of taxonomic instability on conservation efforts (Morrison et al., 2009), and it remains one of the few to do so. A recent study by Simkins et al. (2019) investigated the impact of a recent taxonomic revision (del Hoyo and Collar, 2014, 2016) for birds that resulted in an increase of over 1000 recognised bird species (an increase of 10.7%) over previous estimates. Simkins et al. (2019) looked at extinction risk, protected area coverage, and hotspots of extinction risk, and found that, while this taxonomic revision did lead to a significant increase in the number of bird species in need of protection, it did not necessarily lead to increased extinction risk, reduced protection, or an increase in the number of areas in need of greater protection (Simkins et al., 2019). This work by Simkins et al. (2019) represents the only study that quantitively explores the spatial impact of real-world taxonomic changes on a major clade of organisms. There is therefore a need for more quantitative work into the impact of taxonomy on conservation, not only to test the (often conflicting) assertions of proponents of the PSC (“splitters”) and of the BSC (“lumpers”), but also for conservationists and stakeholders to better understand the impact that taxonomic revision may have on the protection and management of species.

Mammals represent an excellent clade for investigating the impact of different species concepts on conservation planning, because they have played a key role in the species debate, and because they are (together with birds) one of the most intensively studied and best understood clades from a structured perspective (Zachos, 2018). The BSC dates back to the 1930s and remains the most commonly used concept today (Meijaard and Rawson, 2015). Recently, the Phylogenetic Species Concept (PSC) has been increasingly applied to mammals, resulting in a considerable increase in the number of species recognised. An excellent example of this is Groves and Grubb’s (2011) taxonomic revision of the world’s “ungulates” (hoofed mammals), which applied the PSC and resulted in an increase in the number of species from 143 to 279 for the global range of bovid species (Heller et al., 2013). Perhaps unsurprisingly, proponents of the BSC have argued that this near doubling in the number of species in such an historically well-studied and charismatic group as hoofed mammals is a clear case of taxonomic inflation (Heller et al., 2013; Zachos, 2018). Proponents of the PSC have responded that it is a more accurate reflection of species-level diversity within the clade and brings to the fore previously neglected (through taxonomic inertia) and threatened lineages (Gippoliti et al., 2018). The impact that major increases in species number, through the application of the PSC, has on spatial conservation needs exploration. This is important not only for conservation of hoofed mammals (which, regardless of which species concept is used, include many endangered species), but also in the light of a broader need for empiricism in the species concept debate, particularly concerning its impact on conservation.

This chapter quantitatively tests the effect of taxonomic changes on the spatial conservation of one specific group of ungulates, namely African members of the family Bovidae (which include animals such as gazelle, antelope, duikers and wildebeest). Taxonomic changes were represented by creating two different species-level phylogenies of African bovids: one adapted from Upham et al. (2019) that does not include the "new" species recognised by Groves and Grubbs (2011) under the PSC (and so corresponds to a more "lumped" species-level taxonomy), and one that has been modified here to include all of the additional Groves and Grubb (2011) species (and so corresponds to a more "split" species level taxonomy). These phylogenies are referred to here as the "lumped" and "split" trees. These trees were then incorporated into the methodological approach presented in Chapter 4, which optimises the selection of species in space, using MARXAN, for the protection of PD. This is the first study of its kind to directly quantify the impact of different species concepts on a spatial conservation plan.

5.2 METHODS

5.2.1 SPLIT AND LUMPED TREES

This study uses a highly split species-level taxonomy of bovids based on Groves and Grubb's (2011) taxonomic revision, and a taxonomy that represents an alternative phylogeny that does not include the additional species recognised by Groves and Grubb (2011) using PSC-based criteria. Phylogenies for the "split" and "lumped" bovid species-level taxonomies were both built from the 'best' mammal tree from Upham et al. (2019) (4098 species, DNA-only) also used in Chapter 4. The phylogeny for the "lumped" taxonomy was produced directly from the Upham et al. (2019) tree by pruning it to include African bovid species only. This was achieved by using the "drop.tip" function within the *ape* package in R to remove all non-African bovid species. This initial species-level phylogeny of African bovids, which comprised a total of 77 species, was used as the "lumped" phylogeny. There is currently no phylogeny that includes all the 38 additional African bovid species as recognised by Groves and Grubb (2011). The “split” phylogeny was created by manually adding the 38 additional species recognised by Groves and Grubb (2011) in polytomies to the “lumped” phylogeny, using the phylogenetic software package Mesquite 3.61 (Maddison and Maddison, 2019). Each additional species was added to its appropriate location on the phylogeny in a polytomy with the original pre-split species, and then given the branch length that equated to half the branch length of the original pre-split species’ terminal branch length (see Figure 5.1).

5.2.2 SPECIES RANGE DATA

The species range data preparation here utilises the same basic process as the two previous chapters, namely using the IUCN’s global species range shapefile for all terrestrial mammals for which there is adequate data (https://www.iucnredlist.org/resources/grid/spatial-data). This shapefile, and the associated taxonomic information, was clipped to the study region, Africa. Separate shapefiles were created for the range of the two “lumped” and “split” sets of species. This was done by matching the species lists for the phylogeny with that of the IUCN shapefile. This was straightforward for the lumped species list, as all these species are recognised as full species by the IUCN, but this was not the case for the split species, many of which were raised from subspecies to species rank by Groves and Grubb (2011). Fortunately, the IUCN has spatial data for many of these subspecies and thus the lists could be matched to create a shapefile for the split tree as well.

The same sized equal area grid and projection was used here as in Chapter 3 and Chapter 4; a 110km^2 grid and a Behrmann sphere projection. This resulted in 3005 planning units, clipped to the exact extent of Africa, *i.e.* the planning units which intersect the coastline were clipped to coastline itself and were therefore smaller than 110km^2, as with Chapter 3 and Chapter 4 this resulted in accurate ranges of species.

5.2.3 OPTIMISING SELECTION OF SPECIES

The process from this point was identical to that in Chapter 4; optimising the selection of species for PD, for varying amounts of PD (10% intervals up to 100%) using Phylogenetic Diversity Analyzer (PDA) (Chernomor et al., 2015), and then using MARXAN to identify the priority areas to protect these species for each PD interval (see Figure 4.1 in Chapter 4 for a simplified work flow of this analysis). The MARXAN outputs for the “lumped” and “split” phylogenies could then be compared, both qualitatively by eye and also using gap analysis by taking the selection frequencies of the output for one tree away from the other to identify with more certainly where the approaches differ in the priority areas identified.

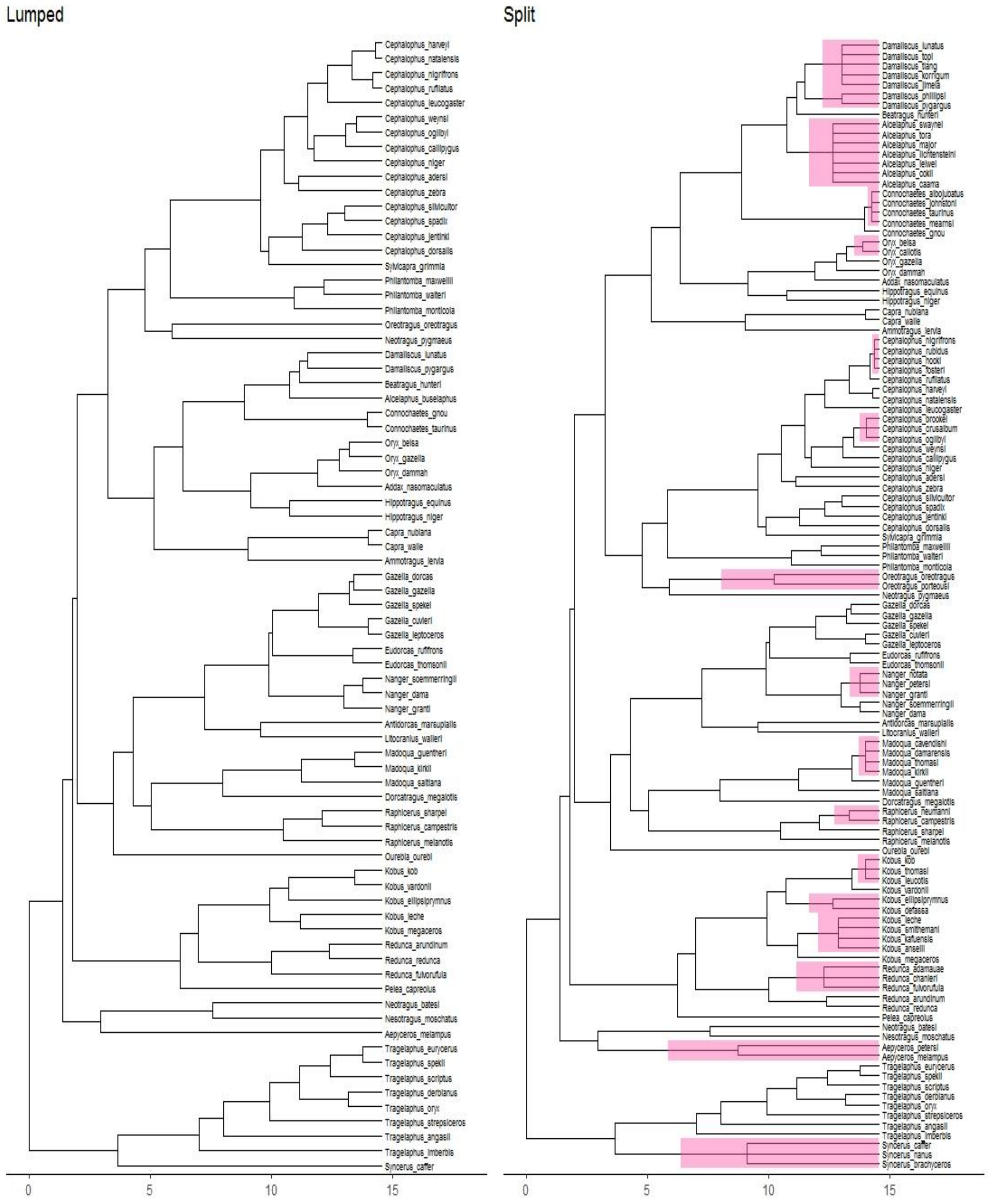

Figure 5.1 Lumped and Split phylogenies. The two trees showing where Groves and Grubb's (2011) additional species were added. The pink highlights where the species were added. Notice that the process results in unresolved branches.

5.3 RESULTS

No major difference between the “split” and “lumped” phylogenies was found in terms of the amount of area required to conserve a given proportion of PD (Figure 5.2). Both trees require a very similar amount of area to optimally protect 10% of their PD, the first PD interval. Both trees then show relatively large increases in area between their 20% and 40% PD intervals, before plateauing slightly. More explicitly, the area required to protect 17% of the range of the species identified for the given PD interval in the “lumped” phylogeny increases by ~5000Km^2 when increasing PD from 30% to 40%, and the “split” phylogeny requires an extra ~9000Km^2 from 20% to 30% PD. After the inflection between 20% and 40%, both phylogenies plateau until they reach 90% PD. To reach this point (from 40% to 90% PD), the “lumped” phylogeny requires only an additional ~8374Km^2 (17% of the area required to protect 100% of its PD), and the “split” phylogeny an additional area of ~6549Km^2 (equating to 13.5% of the 100% PD figure).

Both phylogenies see their largest single (10% PD) increase in area required between 90% and 100% PD – the ”lumped” phylogeny requiring ~32% and the “split” phylogeny ~36% of the total area required to protect 100% of their PD. Both phylogenies require almost the same (within 100Km^2 of each other) amount of area to protect 100% of their PD. The variance in the area required within the different sets of species at each PD interval (represented by shaded area of the line in Figure 5.2) is also very similar between the two phylogenies: the mean average variance in the “lumped” phylogeny is 1633Km^2 and 1735Km^2 in the “split” phylogeny.

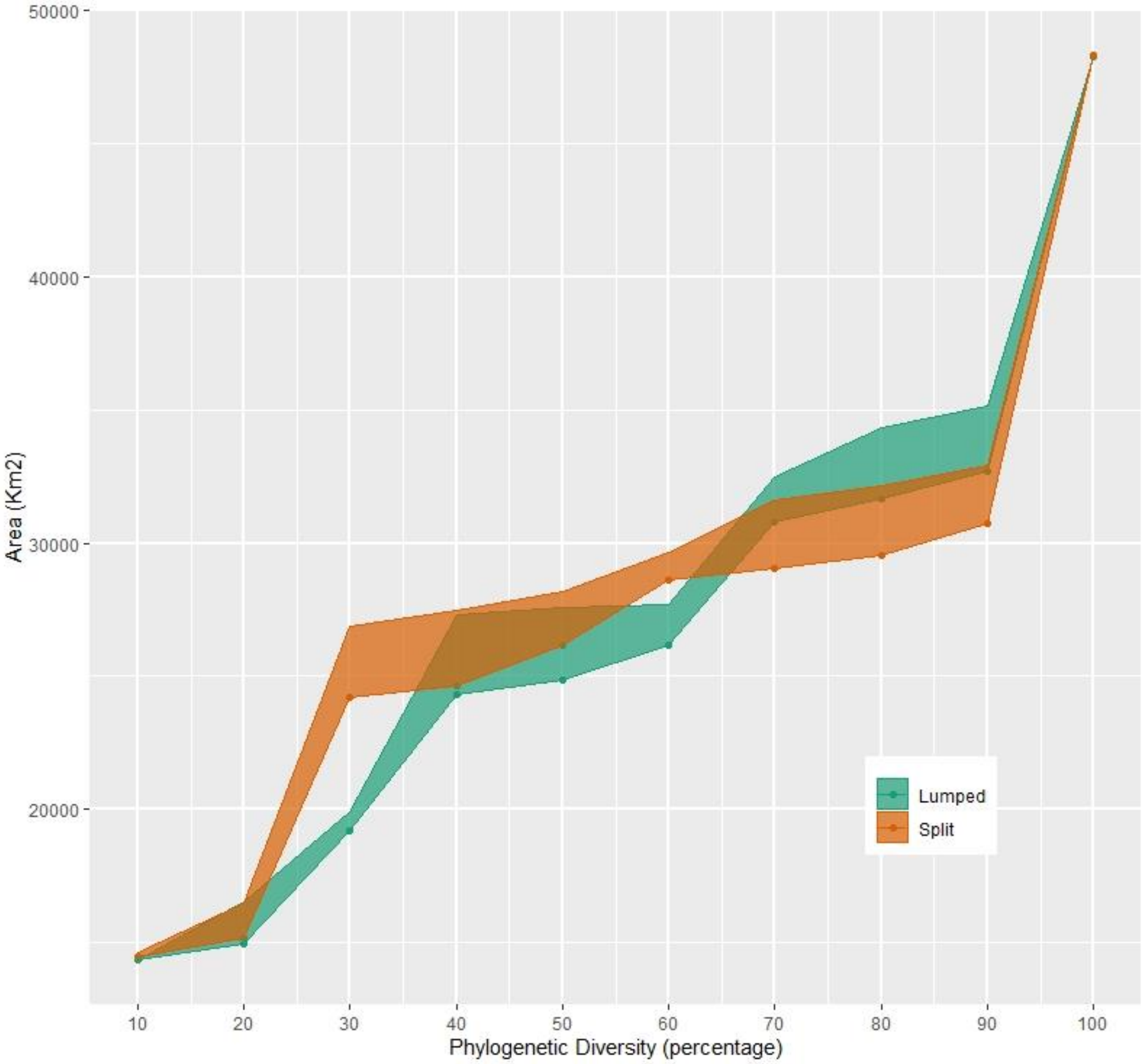

Figure 5.2 The area required to protect Phylogenetic Diversity (PD) for African bovid species. The lower part of the line, with the dots, represents the set of species that required the least amount of area for that tree at that level of PD. The upper part of the line, without any dots, represents the set of species that requires the most land, for that PD interval. The shaded portion of the lines represents the variance in area amongst sets at each PD interval.

In contrast to the area required to conserve a given amount of PD, there are considerable spatial differences in the MARXAN solutions between the “split” and “lumped” phylogenies (Figure 5.3). The spatial differences are relatively minor at the lower PD levels but become more pronounced toward to higher levels. At 30% PD, there is a more homogenous spread of selection frequencies for solutions that are based upon the “split” phylogeny, compared to solutions based on the “lumped” phylogeny where there are discrete areas with higher selection frequencies, resulting in a more heterogeneous pattern of selection frequencies. At 70% PD, major differences begin to become apparent. With areas appearing that are selected within the outputs for the lumped tree but that are not selected at all within any of the MARXAN solutions (n=200) for that set of species, *i.e.* have a selection frequency of 0.

Initially, at 50% PD, these areas are relatively small and with relatively low selection frequencies and are found around the centre of Africa and the north-east coastline (Figure 5.3). The spatial differences between the MARXAN outputs of two phylogenies become more distinct at the higher levels of PD. At 70% and 90% PD, there are large areas selected, with mid-range selection frequencies (50-100), for the lumped phylogeny that are not selected at all for the split phylogeny. These differences are most notable within north Africa between 15°N and 30°N. These areas are slightly fragmented, but represent 4-5 large patches that are not selected at all within the "split" phylogeny, the largest of which centres on roughly 24°N, 15°E. This is further reflected in the fact that the "lumped" phylogeny outputs for 90% PD had over 88,000Km^2 more area with a selection frequency of one or more *i.e.* appeared in at least one MARXAN solution to meet the targets compared to the "split" tree; showing that in this scenario MARXAN had more options to that could meet the targets set.

Figure 5.4 shows the difference in selection frequencies between the outputs of the two phylogenies at the 90% PD interval. This serves to highlight the areas where differences between the two outputs may be finer than what is presented in Figure 5.3, while also further highlighting the disparity between the two MARXAN outputs between the two phylogenies.

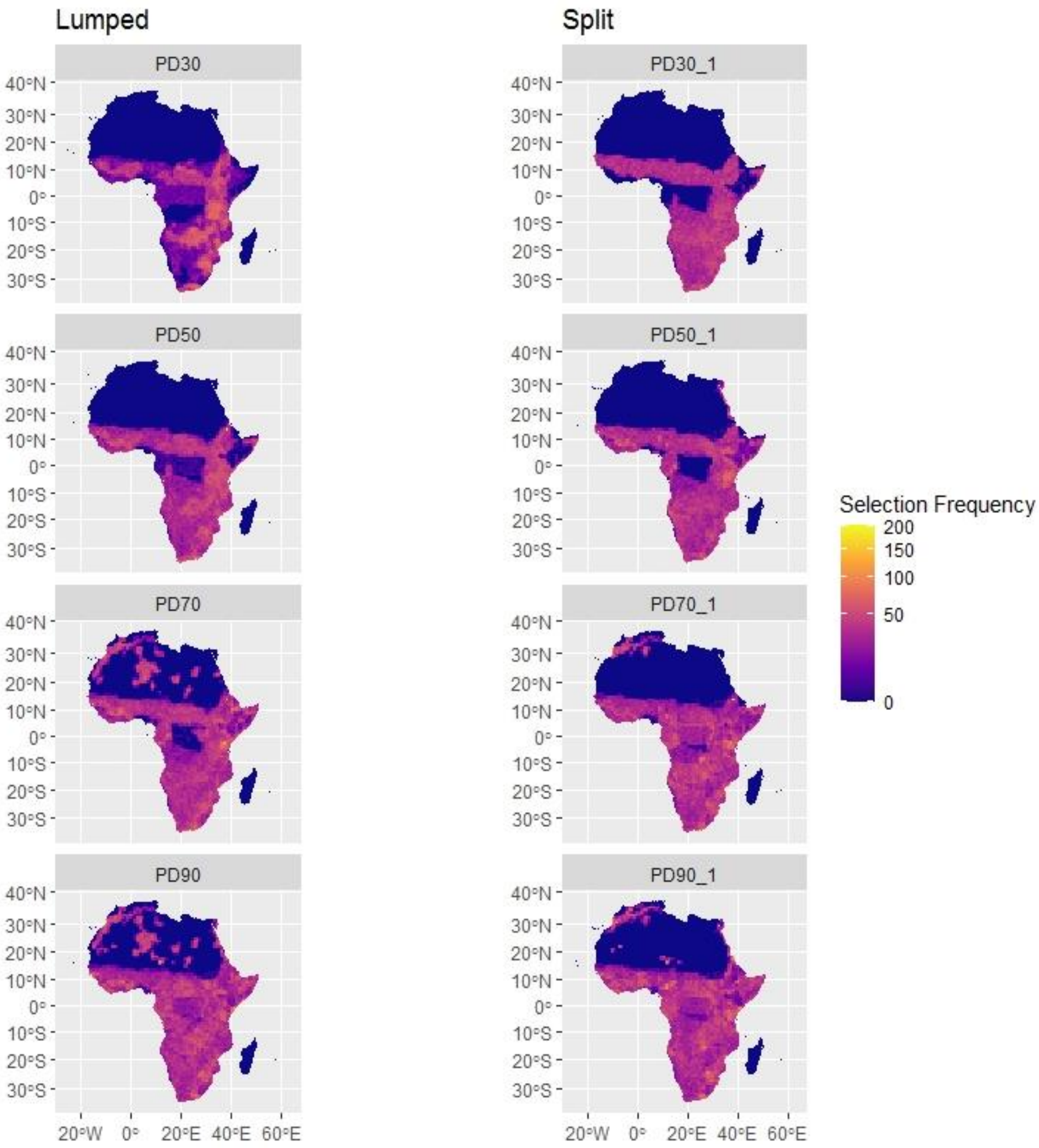

Figure 5.3 Selection frequencies for differing amounts of phylogenetic diversity (PD) for both trees, lumped and split. The selection frequency of the 'best' set, the set requiring the least amount of area (lower line of Figure 5.2) was used for each PD interval. MARXAN was run 200 times for each set, this is reflected in the scale bar. (No data for Madagascar).

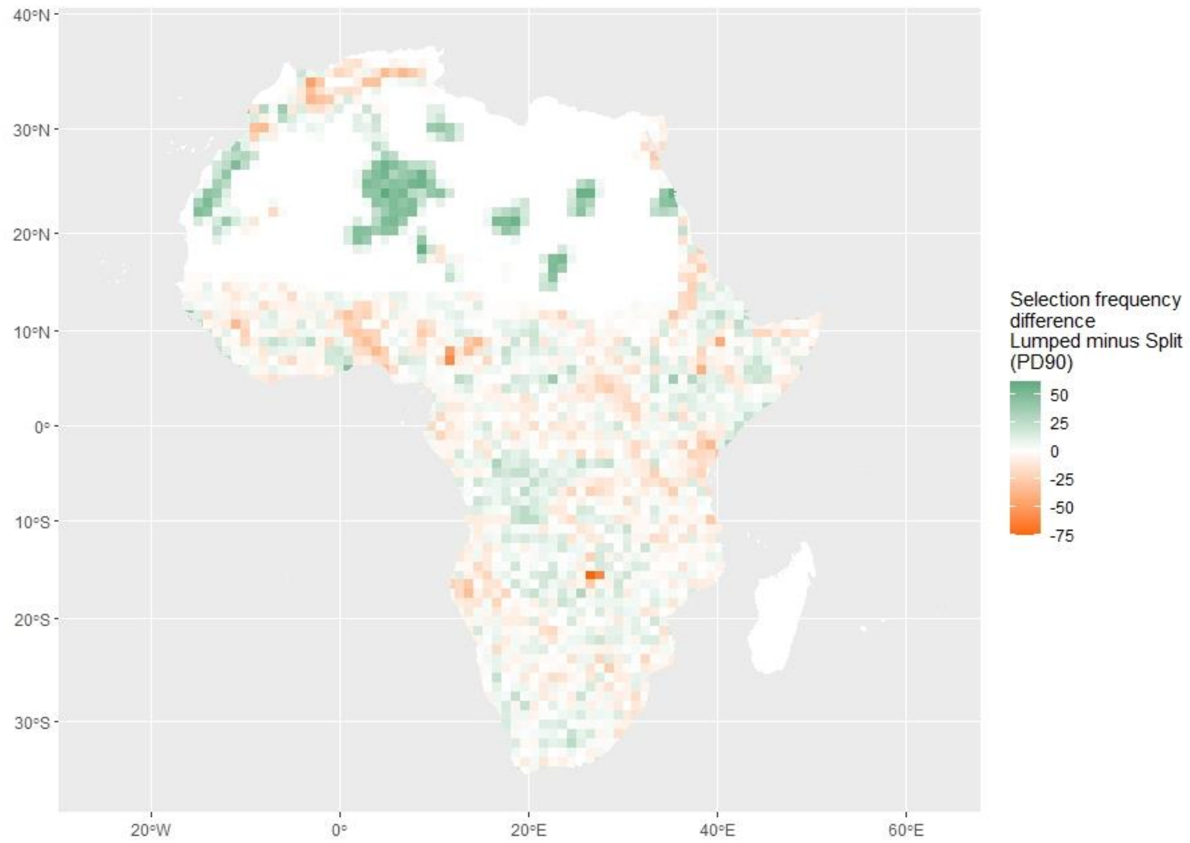

Figure 5.4 Difference map for the selection frequency of MARXAN solutions conserving 90% PD (lumped minus split). The difference map was built by taking the selection frequency values of the split tree away from the lumped tree for each planning unit. Higher values show areas where the lumped tree favoured protecting and the negative values show the areas where the split tree results in higher selection frequencies. (No data for Madagascar).

The differences in the range sizes of the species within each phylogeny was investigated as it was thought here that it may have an important role to play in any spatial found between the spatial solutions generated using the different phylogenies, as a larger range size would provide MARXAN with more options to find solutions. The differences in the ranges of the species between the two phylogenies can be seen clearly in Figure 5.5 and they are significantly different (Mann Whitney U Test: W= 3371, p 0.0051). Perhaps unsurprisingly, the “split” phylogeny has more species with smaller ranges, whilst the “lumped” phylogeny has a more even spread of range sizes with a larger median range size (lumped median range size = 13,072 Km^2, interquartile range = 31,205 Km^2; split median range size = 5160 Km^2, interquartile range = 20,054 Km^2).

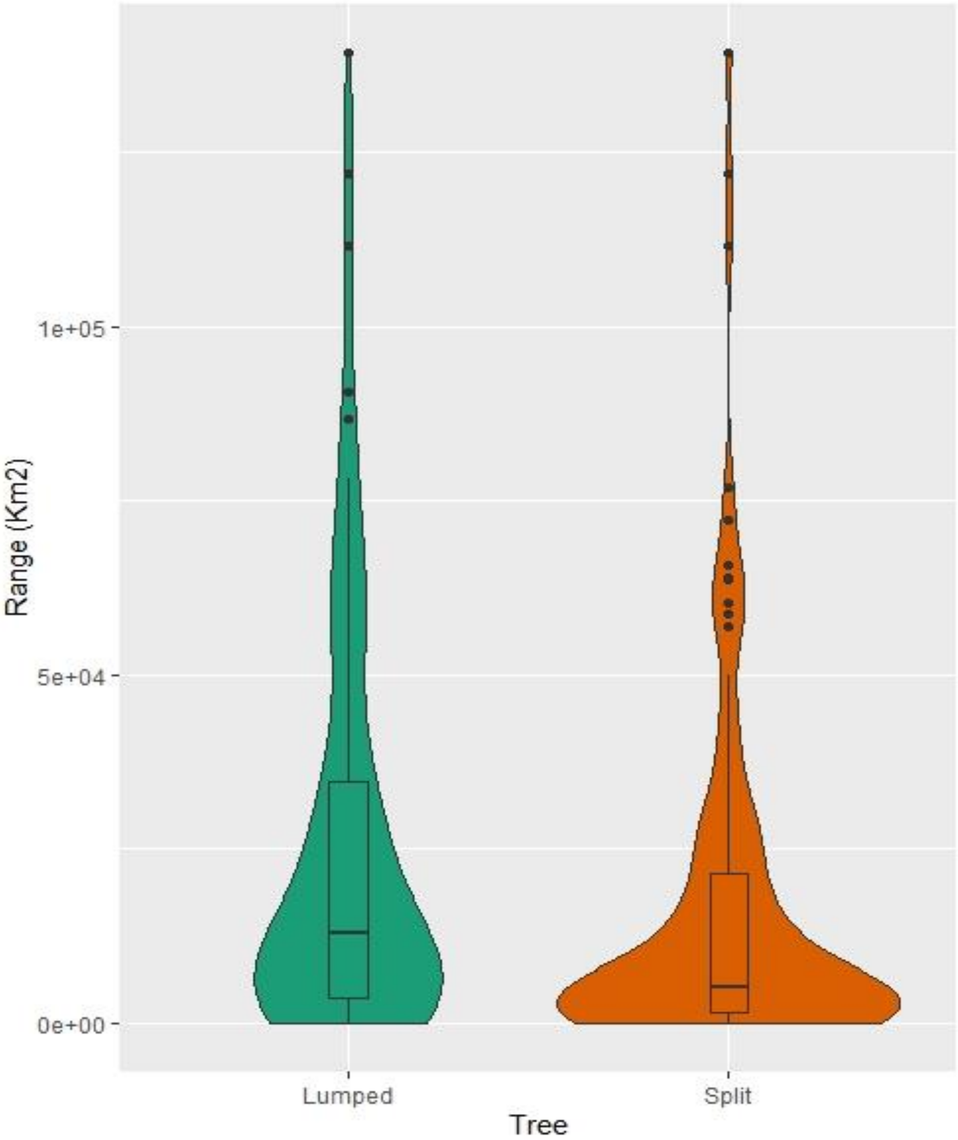

Figure 5.5 Violin boxplots for species ranges for each tree (lumped and split). Boxplot presents 25th, 50th, and 75th percentile with the whiskers showing the smallest and largest values within 1.5 times the interquartile range of the lower and upper quartile, and the outliers are >1.5 times and <3 times the interquartile range beyond either end of the box.

The impact of splitting on the amount of range overlap that occurs amongst species was quantified by calculating species richness at the planning unit level. There was minimal difference in the median range species richness of planning units between the “lumped” and “split” phylogenies (Figure 5.6), the median average and interquartile range being the same between the two phylogenies (median = 7, IQ range = 9), but with the “split” phylogeny having a higher maximum at 29 species.

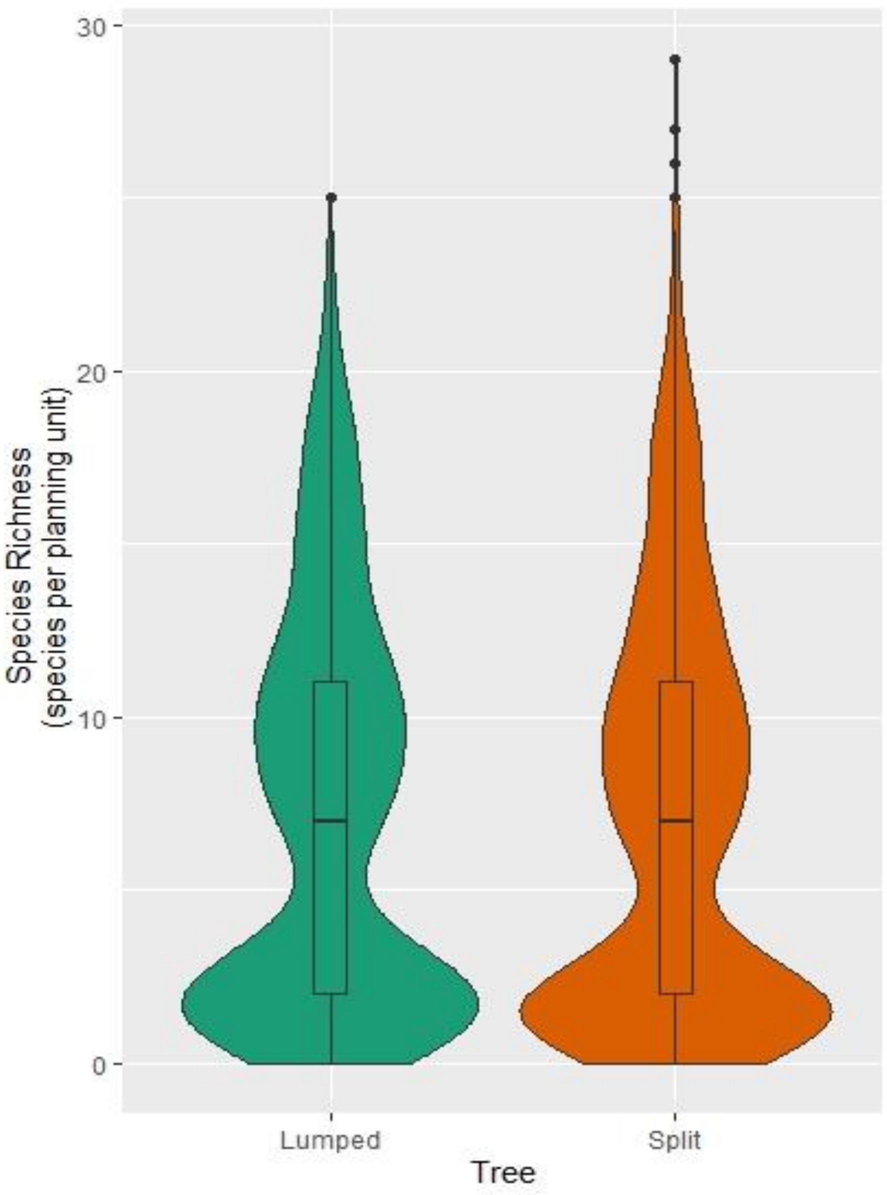

Figure 5.6 Violin boxplots for species richness for each phylogeny (lumped and split). Species richness was calculated as the number of different species present in each planning unit. Boxplot presents 25th, 50th, and 75th percentile with the whiskers showing the smallest and largest values within 1.5 times the interquartile range of the lower and upper quartile, and the outliers are >1.5 times and <3 times the interquartile range beyond either end of the box.

5.4 DISCUSSION

The impact of taxonomic revision based on the Phylogenetic Species Concept (PSC), leading to an increase in the number of species (aka “splitting”) on spatial conservation planning was explored in this chapter, using African bovid species as a test case. Through the application of the methodological approach presented in Chapter 4, which optimises species selection across space for the protection of PD, it has been shown that increases in the number of species recognised as valid (“splitting”) can cause substantial changes to the location of priority conservation areas. However, use of a “lumped” versus a “split” species-level phylogeny did not substantially affect the total area required to achieve the conservation objectives (% PD represented in network).

The results here show that “splitting” can have a substantial impact on the location of the areas required to protect a given level of PD for African bovids. Despite much assertion in the literature of the impact of different taxonomic approaches, this study is only the second to quantitatively assess the spatial implications of major taxonomic revisions on a whole clade of organisms, the other being on birds by Simkins et al. (2019). The spatial differences shown between the “split” and “lumped” phylogenies used here varied with the amount of PD targeted, with the greatest differences seen at higher PD levels. When PD was protected at 70% and above, the MARXAN outputs for the lumped phylogeny showed areas of high selection frequency in North Africa that were not selected at all in the outputs for the split phylogeny, *i.e.* the phylogeny with more species. This finding was initially surprising, as it may be intuitive to expect that a phylogeny with more species would result in a MARXAN output that had more planning units with a selection frequency above 0, which is the opposite to what was found here. However, this result may in fact be a common consequence of splitting clades using the PSC. Specifically, the splitting of African bovid species using the PSC (Groves and Grubb, 2011) markedly reduced the median range size of species by over 50%. This reduced range size is associated with how the PSC is applied. Groves and Grubb’s (2011) implementation of the PSC implicitly took into account geographic separation through the identification of the smallest population level group (Groves and Grubb, 2011). While the PSC does not look to define all individual populations as different species, by focussing on identifying heritable differences between populations, differences that may be morphological, physiological, behavioural or molecular, the application of the PSC is more likely to result in the identification of more species than the BSC (Zachos, 2015) with the new species less likely to have overlapping ranges. Subsequently, this impacts how MARXAN operates when trying to meet spatial targets for “lumped” (= applying the BSC) and “split” (= applying the PSC) phylogenies. The split phylogeny has more species, with smaller ranges that are less likely to overlap, and therefore limits MARXAN’s potential solutions more than with the lumped phylogeny, with its larger species ranges and greater likelihood of overlapping ranges. Smaller ranges also mean that proportional targets, as used here, can be met with less area. This impact of splitting means that MARXAN has fewer options to find solutions that meet the targets set, with more spatial specificity in the optimal solutions it can find, which may result in fewer options for planners and stakeholders to explore.

With the main aim of this chapter being, for the first time, to identify the impact of taxonomic changes on a spatial conversation planning exercise, it was important to view the results as broadly as possible; this is why selection frequencies were used as the predominant data for comparison. As previously discussed, MARXAN does not provide deterministic outputs (which gives it flexibility) and to choose two outputs to compare out of a possible 400 (200 runs per scenario), particularly without the context of previous case studies, may result in much of the story being missed, or missed reported, hence selection frequencies were used as they provide a fuller picture. Broadly speaking, for example, in this chapter all of the split species did in fact intersect a planning unit that was selected in at least one (out of 200) possible solution in both scenarios at the 90% PD interval. However, the level of protection will fluctuate dependant on which solution is chosen. Now that it has been proven here, for the first time, that taxonomic changes can have substantial impacts on spatial conservation plans, further work is needed, using more case specific scenarios, to explore the impact in more detail.

The use of consistent proportional target setting is important to discuss. While it is the dominant approach within the, albeit limited, literature (Carta et al., 2019; Rosauer et al., 2017; 2018) and therefore adopted here, with 17% used as it reflects the CBD's 2020 protected area targets (CBD https://www.cbd.int/sp/targets/rationale/target-11/), it does have some limitations when it comes to the comparison of different scenarios. With a variation in range size between split and lumped species, proportional targets result in differences in area demand for MARXAN. However, in order to increase the confidence of direct comparisons between scenarios, the species penalty factors can be, as they were here, set the same in each scenario meaning that the equivalent weight is put on meeting representation targets, an approach used by Rosauer et al. (2017). While in a more real-world scenario stakeholders would likely adjust all the coverage targets in a bespoke species by species/case by case approach, further work is needed, in the context of the comparisons here and elsewhere in the literature, on the impact that proportional target setting can have on comparisons between different scenarios.

Although there was a difference in the location of protected areas when using the split or the lumped phylogenies of African bovids, there was no substantial difference in the amount of area needed to meet phylogenetic based conservation targets. Again, this is likely a result of the geographic basis for the splitting of species by the PSC, compared to the BSC, as applied by Groves and Grubb (2011). Species split in this way, using the PSC, will have smaller ranges, meaning that proportional targets can be met with less land. However, given there are more species in a split situation, and these species are less likely to have overlapping ranges, any savings in the amount of land required to meet proportional targets, is likely off-set, to some degree, by the reduced complementarity; in this example it may have ultimately cancelled out any differences, although further investigation would be required to assess if this was the sole cause of the similarities in the size of the planning areas between the two phylogenies. Despite the spatial differences in the outputs between the split and the lumped phylogenies, it is important to note that it is possible, in this example, to conserve both sets of species with a similar amount of land. However, this chapter is the only worked example of the impact of splitting on the spatial conservation of a clade and the relationship this has with range size and the area required for protection. The same may not be the case with other clades with different patterns of distribution, which may be impacted differently dependent on the way the clade was split or lumped.

Taxonomic changes due to different species concepts made minimal impact on the overall species richness of African bovids per planning unit. This result is perhaps counterintuitive, as the split phylogeny (PSC-based) has 38 more species, but once again this points to the non-overlapping nature of the species ranges of the spilt phylogeny. There are some planning units where there is disparity in the number of species found dependent on the phylogeny used, but these areas are either very small or the disparity is very low, or both.

In light of the limited number of empirical studies that investigate the, much debated, impact of taxonomic revisions (particularly those that result through application of the PSC, which tends to increase the number of species recognised) on conservation, this study adds some much-needed quantitative data; it is also the first to look explicitly at the impact of this on spatial conservation planning. Agapow et al. (2004) reported that an adoption of the PSC could result in an up-ranking of subspecies to species that would result in an increase in global species by ~48%, as well as a general likelihood for decreases in species ranges and also an increase in the number of endangered species. While changes to the threat level of African bovids was not investigated here, substantial decreases in species ranges were seen with application of the more heavily split, PSC-informed species level taxonomy of Groves and Grubb (2011), which would likely result in some amount of threat level change. Changes in threat level due to taxonomic changes have been reported in the literature (Agapow et al., 2004; Domínguez Lozano et al., 2007; Garnett et al., 2003), but these are mainly associated with the simple upgrading or downgrading of a species' endangerment level and do not necessarily result in changes to the actual level of conservation a particular species is afforded due to a taxonomic revision. Morrison et al. (2009) addressed this issue by investigating the impact of taxonomic change on the level of conservation provided to species, using 19 different examples across the world where the level of protection afforded to a species or population had changed due to taxonomic revisions, and found no consistent impact. This was something echoed in the results of Simkins et al. (2019), whose work on global bird species found that, while major taxonomic revisions resulted in an increase in the number of species requiring conservation, there was no consistent impact on the extinction risk across bird species, nor on the level of protection provided by protected areas. However, the results presented here using African bovid species as a case study show clear and consistent evidence that major taxonomic revision can have substantial impacts of spatial conservation in terms of the location of priory areas for conservation. Given that a plurality of species definitions is likely to remain in the conservation world for the foreseeable future (Agapow et al., 2004), it is important for conservationists to be aware of the impact on spatial conservation in particular, as the use of protected areas continues to be a cornerstone of global conservation strategies (CBD 2020 https://www.cbd.int/protected/).

The results from this chapter also shine an important light on the resilience of PD-based conservation approaches to taxonomic changes. It has been suggested in the literature that PD-based approaches will be more resilient to taxonomic changes; splitting, for example, resulting in relatively small additions to overall PD in comparison to species richness (Faith, 2002; Isaac et al., 2004; Diniz-Filho et al., 2013). However, the results from this chapter, the first of their kind, show that taxonomic changes can have a substantial impact on spatial conservation outcomes even when a PD approach is applied. Further work should look to ascertain the extent to which PD-based approaches are impacted by taxonomic changes relative to species-based methods.

This is the first study to explore the implications of major taxonomic revisions based on application of the PSC on spatial conservation planning. The results show just how impactful taxonomic changes can be to the location of conservation areas identified within a spatial conservation plan. This chapter is part of a, currently, very small but important body of work looking to quantitively explore the impact of taxonomic inconsistencies on conservation. In a world in which different species concepts continue to be used, resulting in very different species-level taxonomies, this is something that requires considerable further study.

CHAPTER 6 DISCUSSION

The overarching aim of this thesis is to facilitate, and to develop improved methods for, the integration of evolutionary considerations into biodiversity conservation. This has been achieved firstly via a review of previous studies that have incorporated phylogenetic diversity (PD) into optimised spatial conservation planning (Chapter 2). Three research chapters then collectively explore the impact of incorporating PD on conservation planning and propose novel approaches for doing so, using a range of different mammalian clades as case studies (Chapter 3, Chapter 4, and Chapter 5). The key findings of this thesis are summarised below.

The literature review presented in Chapter 2 shows that there are still relatively few case studies investigating the use of PD-informed spatial conservation planning. The review revealed consistent evidence of mismatching between priority areas selected to maximise the conservation of PD and those selected to maximise species richness, but that this alone is not evidence either for or against surrogacy between the two measures, which is in itself greatly understudied. There is a need for more case studies using MARXAN, which is an effective and widely used tool for spatial conservation planning that nevertheless has been relatively ignored within this field in favour of Zonation. This is likely due the relative ease with which Zonation can be used, when compared to MARXAN, within a case-study specifically to compare planning outputs between approaches that have used two different metrics for prioritisation. However, MARXAN, in not using such a deterministic approach, has more flexibility to find multiple alternative solutions that meet a planner’s targets, which may make it a more attractive tool for planners (Chapter 2). Chapter 3 shows that there are spatial differences between planning outputs for the conservation of PD and those from a species-driven approach for the conservation of primates (monkeys, apes, lemurs, etc.). These mismatches are strongly influenced by the amount of area the planning solution is constrained by: as available area decreases, spatial mismatch between PD-informed and species-informed priority area increases (Chapter 3). Despite spatial mismatches in priority areas, a species-based approach to spatial conservation planning captures a very similar amount of PD when compared to a PD-led approach for primates. This suggests that, for primates, species richness may act as a suitable surrogate for PD (Chapter 3). Using a novel method that utilises a greedy algorithm for the selection of species to maximise PD it is shown, in Chapter 4, that species can act as the conservation features around which PD-led conservation efforts can be based, in contrast to previous published methods for incorporating PD into conservation planning, where the conservation features are phylogenetic branches weighted to represent their length. By accounting for PD before the spatial optimisation element, *e.g.* the use of MARXAN, this novel approach, presented in Chapter 4, removes the issue of having to constrain the area within which a solution can be found, something that has be shown to influence how strongly a solution favours the inclusion of PD (Chapter 3 and Rosauer et al., 2017). This new method also allows planners to continue to use species as conservation features, which has been the traditional and more widely used approach, compared to the use of phylogenetic branches; this may in turn lead to an increase in the use of PD-informed approaches within conservation planning. Chapter 5 shows that changes in species-level taxonomy can have substantial impacts on spatial planning outcomes, using African bovid species (gazelles, antelopes etc.). Specifically, when applying the novel PD-informed spatial planning method presented in Chapter 4 to African bovids, the locations of planning outcomes differ markedly depending on whether or not a recent species-level taxonomy that applies Phylogenetic Species Concept (Groves and Grubb (2011) is used.

Overall, this thesis shows that PD can be successfully incorporated into conservation planning, that it has a major impact on spatial planning outcomes, particularly when resources (in this case, area) are limited, and that there is a need for future work to investigate the potential for surrogate metrics and integrated approaches that account for the multidimensional characteristics of biodiversity.

6.1 GENERAL DISCUSSION

The question of exactly what to protect is a central issue in the field of conservation, and one which is inevitable given limitations (*e.g.* financial, spatial) in resources. The evidence linking the protection of evolutionary history to human-centric benefits has been argued to be relatively tenuous (Tucker et al., 2019). However, it is not the aim of this thesis to delve too deeply into the debate (some of which is philosophical) around what elements of biodiversity to protect over others; it is, instead, to undertake a detailed investigation into the effect of incorporating evolutionarily-informed metrics, specifically PD into biodiversity conservation. PD is becoming increasingly valued by many influential conservation organisations, directives, and also within the peer-reviewed literature (Tucker et al., 2019).

For example, the awareness of the importance of PD for informing conservation decisions drove the creation in 2019 of a ‘Phylogenetic Diversity Task Force’ by the International Union for Conservation of Nature’s Species Survival Commission (IUCN SSC) (https://www.iucn.org/commissions/ssc-groups/cross-cutting/phylogenetic-diversity-task-force). Similarly, the Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services (IPBES) cites PD as an important factor to measure the value of the environment to global populations (IPBES, 2018).

Multiple authors have argued for the importance of evolutionary history to the conservation of biodiversity (Vane-Wright et al, 1991; Faith, 1992; Crandall et al., 2000; Moritz, 2002; Ashley et al., 2003; Santamaría and Méndez, 2012), but the explicit inclusion of evolutionary metrics within conservation is rare, with taxonomic metrics such as species richness being favoured instead (Brooks et al., 2006; Brum et al., 2017). The data required to calculate PD, namely suitably comprehensive phylogenies with associated branch lengths, is becoming increasingly available (*e.g.* Bininda-Emonds et al., 2007; Prum et al., 2015; Jetz and Pyron, 2018; Upham et al., 2019). Given the availability of suitable methods and data for incorporating evolutionary considerations into conservation planning, the general lack of studies that do so requires urgent investigation, particularly when biodiversity is being lost at an unprecedented rate and unevenly across the tree of life with the many evolutionary distinct taxa also being the most at risk of extinction (Purvis et al., 2000).

6.1.1 THE EMERGING FIELD OF PD-INFORMED CONSERVATION

Since Faith (1992) first introduced the concept, 845 published papers have discussed the relevance of PD to conservation, of which ~50% have been published since 2016, highlighting the timeliness of this thesis. The review in Chapter 2 demonstrates that the incorporation of PD into optimised spatial conservation planning is an emerging field. The review identified 13 studies in which PD has been successfully incorporated into existing, widely used spatial optimisation methodologies, most of which implemented via Zonation and (to a lesser degree) MARXAN. Of the 13 case studies identified in the review, only five used MARXAN, despite MARXAN being the world’s most widely use software for the planning of protected areas (Ball, Possingham and Watt, 2009; Watts et al., 2017). Of these, only two used MARXAN to compare PD and species-based approaches; the lack of case studies highlighting the need for further work.

MARXAN's ability to set bespoke targets, alongside its stochastic approach gives it enormous flexibility and therefore utility. However, it is important to look beyond MARXAN, and to explore if MARXAN still in the best tool for the job. Prioritizr represents a newer tool in the development of approaches to solve conservation planning problems. Prioritizr uses integer linear programming which, unlike the simulated annealing used by MARXAN, is guaranteed to find optimal solutions. Prioritizr is also able to solve problems using input data formatted for MARXAN (https://prioritizr.net/index.html; Rosauer et al., 2017). However, for situations that involve multiple scenarios, as with the work in this thesis, Prioritizr is much slower than MARXAN (Rosauer et al., 2017). Prioritizr can however be used to compare the optimisation performance of MARXAN solutions as Prioritizr will specify a level of optimality (Pollock et al., 2020). MARXAN therefore remains one of the most useful tools in the field of spatial conservation planning, particularly when it comes to processing numerous different sets of input data; however, the advent of new tools, such as Prioritizr can add to the decision making power of stakeholder.

6.1.2 A NOVEL WEIGHTED BRANCH-BASED APPROACH FOR INCORPORATING PD INTO SPATIAL CONSERVATION PLANNING

Collectively, the findings of the review provided the impetus for Chapter 3, which addressed the lack of studies, by providing a case study of an ecologically diverse and widespread mammalian clade that includes numerous threatened and endangered species, namely the order Primates (monkeys, apes, lemurs, bushbabies, tarsiers, etc.). Chapter 3 presents the first, and currently only, spatial conservation planning exercise case study using an optimised approach to identify priority areas, *i.e.* using a spatial conservation tool with an optimisation algorithm (in this case MARXAN), for the conservation of primate PD. It serves as a useful case study for the currently understudied but rapidly growing field of evolutionarily-focussed spatial conservation, and includes an investigation into the potential for species richness to act as a surrogate metric for PD. As well as providing insight into the priority areas for maximising the conservation of primate evolutionary history, results from Chapter 3 show that the relative amount of area available for the conservation plan to find solutions within impacts the amount of spatial mismatch between priority areas for PD and those for selected using a more traditional species-based approach. This is perhaps an unsurprising result, as it is known that there are differences in the spatial patterns of PD and species richness (Forest et al., 2007) so as the constraints increase on MARXAN *i.e.* the amount of available area is decreased, the weightings of the conservation features - which in the case of the PD-led approach used in this chapter are proportional to the lengths of the branches - have greater influence. As a result, any spatial differences become emphasised in the selection frequencies of the planning units *i.e.* the priority areas. Nevertheless, the results from Chapter 3 explicitly casts doubt on the suitability of using a penalty (applied proportionately to account for the varying amounts of PD represented by different branch lengths) to account for PD in a conservation plan, with the impact of limiting available area seemingly influencing how strongly PD is protected within a plan, when compared to a species-based approach. The method of requiring that the amount area be limited, in order to account for PD, is achieved through an approximation by applying a 'cost threshold' in MARXAN's input file. The use of the 'cost threshold' allows MARXAN, which has an algorithm designed to solve a 'minimum set problem', to instead solve a 'maximum coverage problem'. This approach has been used by Rosauer et al. (2017), in a case study on the conservation of PD for mammals globally, and by Carta et al. (2019) who used the approach in a phylogenetically informed conservation planning exercise for threatened plant species in the Mediterranean. The use of MARXAN in the approach provides benefits associated with flexibility, when compared to Zonation (which is designed to solve a 'maximum coverage problem'), which unlike MARXAN is deterministic in its approach. However, the use of the 'cost threshold' setting on MARXAN is known, in some cases, to produce sub-optimal results (Ball and Possingham, 2000).

6.1.3 IS SPECIES RICHNESS AN EFFECTIVE SURROGATE FOR PD?

Evidence for surrogacy between PD and species richness, is a key question because, although phylogenetic data sets and methods are becoming more accessible, data on species richness is likely to always be more comprehensive and easier to obtain. Therefore, if species richness is indeed an effective surrogate for PD, then conservation plans that attempt to optimise the protection of evolutionary history may not have to delay their implementation or adjust their current design while waiting for robust phylogenetic data to be made available for analysis (Rapacciuolo et al., 2019).

Of the studies identified within the review in Chapter 3 (n=13), which were selected for their incorporation of PD within a spatial conservation planning exercise, there was consistent evidence of spatial mismatches in the priority areas identified for PD when compared to those for species richness. However, despite studies elsewhere in the literature reporting that mismatches in spatial patterns of diversity (Devictor et al., 2010; Zupan et al., 2014) and priority conservation areas between PD and species richness (Sobral et al., 2014; Brum et al., 2017) are evidence for poor surrogacy, this is not, in fact, the case (Rodrigues and Brooks, 2007; Rapacciuolo et al., 2019). Surrogacy is measured as the amount of one metric, *e.g.* PD, that is captured within a conservation plan designed to capture another *e.g.* species richness (Rapacciuolo et al., 2019). This being the case, there is only very limited evidence that species richness could act as a surrogate for PD within the studies identified in the review in Chapter 3. Only two studies, Rosauer et al*.*(2017) & Rapacciuolo et al*.* (2019), actually presented analyses of the amount of PD captured within a species-based approach. Rosauer et al*.* (2017) reporting that species are a poor surrogate for PD in a study of the world's mammals, although their results show that this is dependent on the amount of available area, with the increases in surrogacy found when the solutions were less constrained by available area. By contrast, Rapacciuolo et al*.* (2019) reported that, for 10,213 terrestrial vertebrates occurring across the Americas, species richness-based conservation could be sufficient to preserve much of the phylogenetic dimension of biodiversity.

Chapter 3 also provides important new data that bears on the debate regarding the surrogacy potential (or not) of different metrics. Specifically, Chapter 3's analysis of primates showed that, despite spatial differences in planning outputs, species-based plans captured almost the same amount of PD as PD-based plans. This result in Chapter 3 and work by Rapacciuolo et al. (2019) shows that species richness has the potential to act as a suitable surrogate for PD. However, there is a great deal more work needed within the field of surrogate metrics, not least because there are only a few studies, and it is likely that the degree of surrogacy will be case-specific. Chapter 3 only looked at primates, whilst Rapacciuolo et al. (2019) considered only terrestrial vertebrates of the Americas, and it is unclear that similar results would be obtained when considering other groups of organisms. There is also a risk associated with surrogates if they are poorly understood; policy makers may discount the need for additional efforts to account for evolutionary history if they believe it can be successfully included within species-based approaches. While the results of Chapter 3 show that, in the case of primates at least, similar amounts of PD are captured by a species-based approach as by a PD-led approach, it does not account for which parts of the phylogeny are captured; three branches representing 10 million years of evolutionary history each will be treated the same as one branch of 30 million years. There is the potential for major parts of evolutionary history to be unknowingly missed when relying on surrogacy in this way.

6.1.4 A NEW APPROACH

The potential issues with the weighted branch-based approach for incorporating PD into optimised spatial conservation planning that was used in Chapter 3, and the current lack of alternative approaches, drove the creation of the novel approach presented in Chapter 4. This approach successfully accounts for, and utilises, the different amounts of evolutionary history represented by species in a MARXAN approach that does not rely on penalties or thresholds; it does this by using species as the conservation features in the conservation plan, and accounts for PD prior to the MARXAN element of the method. PD is accounted for in isolation, via the greedy algorithm within PDA (Chernomor et al., 2015) that selects sets of species that maximise PD; these sets can then be used to set coverage targets in MARXAN. The solutions can then be analysed in MARXAN to identify the optimum set (or sets) of species for a given amount of PD, either by finding the cheapest solution, *e.g.* the plan that contained the least area in this case, or via the use of further metrics, for example, taking into account the threat level of the species in each set. By using species as conservation features, and accounting for PD in isolation, this methodology represents an approach that is simpler than the weighted branch-based approach, and with less chance of sub-optimal outcomes that may be difficult to detect within MARXAN's outputs. In addition to this new method, Chapter 4 also highlights the differences in spatial planning outputs between three species-rich mammalian clades (the orders Artiodactyla, Carnivora, and Primates), and how these differences may be hidden when trying to conserve a large clade. For example, the results show that each of the three mammalian clades considered had a different relationship between the amount of PD protected and the area required to do so, and such differences would likely be lost if the three clades were analysed as one.

6.1.5 THE IMPACT OF CHANGES IN SPECIES-LEVEL TAXONOMY ON CONSERVATION PLANNING

Species play a central role in conservation planning; this is true even when using a PD-led approach, as PD is typically calculated based on species-level phylogenies. A key question is therefore what units of biodiversity should be recognised as a distinct species. The debate, however, concerning the definition of a species is still far from reaching a consensus, with much current discussion about whether or not the PSC (which typically results in the recognition of a greater number of species than other species concepts) should be used (Gippoliti, 2019; Taylor, Denys and Cotterill, 2019; Zachos, 2019; McClure et al., 2020). The impact of differences in taxonomic practice (particularly use or not of the PSC) to conservation is therefore important to understand, and is something that is still debated within the scientific literature (Garnett & Christidis, 2017; Gippoliti & Groves, 2018; Zachos, 2018).

Despite this often fevered debate, few studies have actually attempted to investigate the impact of taxonomic changes on conservation planning using real-world case-studies (Simkins et al., 2019). Whether a species is recognised or not as a distinct terminal branch within a phylogeny may impact PD-based conservation efforts but is also likely to have implications for the conservation of biodiversity more broadly. Chapter 5 aimed to address this gap in the scientific literature by investigating the impact of changes in species-level taxonomy to conservation planning, specifically PD-based conservation planning for African members of the family Bovidae (which includes antelope, gazelle, duikers, wildebeest and relatives). This family was chosen because a recent PSC-based classification (Groves and Grubb, 2011) is available that results in a large increase on the number of species recognised, from 143 to 279 for the global range of bovid species. The results showed, using African bovids as real-world case-study, that species-level taxonomic changes can have a substantial impact on the location of priority areas for conservation, with large areas of North Africa not selected at all within MARXAN’s 200 best solutions for the “split” (PSC-based) phylogeny when compared to the “lumped” (non-PSC-based) phylogeny. However, while the location of priority areas for African bovids changed as a function of using a more heavily “split” species taxonomy, the amount of area did not change. The distinction between the impact taxonomic changes have on the location versus the size of the priority areas in these results is important. Reporting substantial changes in the location of spatial conservation plans may be misinterpreted as impacting the cost of a plan; while this may be the case in reality, in the case of African bovids there was no significant change in cost (as measured by area) as a result of taxonomic differences. However, it is important to stress that, within the spatial differences, not only did the priority areas differ, but the ability for MARXAN to find different solutions (one of its core benefits) was impacted by taxonomic changes. The increase in the number of species via the application of the PSC truncated the species ranges, and likely reduced the amount of overlapping ranges as a result, meaning reduced flexibility when finding optimised solutions when compared to the more “lumped” phylogeny that did not use the PSC. The reduction in the amount of the planning area that can be used to meet the targets as a result of the splitting, in this example at least, may, in turn, limit the ability of planners to find optimal solutions that work best for all stakeholders. Conservation of PD is cited as being more resilient to taxonomic changes compared to approaches that focus on species richness (Isaac et al., 2004; Diniz-Filho et al., 2013); this requires further investigation as the results from Chapter 5 show that changes to species taxonomy (specifically those that result from implementation of the PSC) does have a substantial effect on PD-based conservation approaches, at least in the case of African bovids.

6.1.6 THE POTENTIAL FOR INCORPORATING ALTERNATIVE METRICS INTO SPATIAL CONSERVATION PLANNING

There are numerous other metrics, besides PD, that also have the aim of recognising previously unrepresented and under-investigated elements of biodiversity, both within the broad concept of “evolutionary considerations” and outside it. Of these other metrics, those that aim to incorporate evolutionary considerations include Phylogenetic Endemism and Evolutionary Distinctiveness. Both of these metrics are closely linked to phylogenetic diversity: Phylogenetic Endemism was presented by Rosauer et al. (2009) and combines PD with a weighted endemism measure to help identify areas where substantial components of PD are restricted. Evolutionary Distinctiveness, meanwhile, measures how “isolated” species are within a clade, and can be used deterministically to create a rank order of distinctiveness. Jetz et al. (2014) combined Evolutionary Distinctiveness with species range data to produce a new combined metric of Evolutionary Distinctness Rarity, which, as the name suggests, weights both Evolutionary Distinctiveness and rarity (calculated as global geographic range size) together, to produce a new rank order to guide decision makers. Perhaps the most well-known combination metric that falls under the evolutionary umbrella is the Evolutionarily Distinct and Globally Endangered (species), or EDGE, metric developed by the Zoological Society of London (Isaac et al., 2007). The EDGE metric aims to help decision makers identify species that should be priority conservation targets based on a combination of their evolutionary distinctiveness and their current conservation or endangerment status. The EDGE programme has helped implement over 100 conservation projects, although it takes a species by species approach, and as such has not been integrated into an optimised spatial conservation planning exercise (https://www.edgeofexistence.org/).

There is a pressing need for more integrated approaches to conservation that capture the multifaceted nature of biodiversity. This is exemplified in the literature by the continued efforts to develop new and improved metrics that incorporate evolutionary and other considerations. Farooq et al. (2020) recently published an updated version of the EDGE metric: Weighted Endemism including Global Endangerment index (WEGE), includes a weighted endemism measure that allows for areas to be ranked in accordance with Key Biodiversity Areas developed by the IUCN (IUCN, 2016). Gumbs et al. (2020) have developed two new PD metrics that combine PD and human pressure across the range of a species; the first is Human Impacted Phylogenetic Endemism (HIPE), which is an extension to phylogenetic endism that weighs phylogenetic branches in space in relation to human pressure, which is measured using the Human Footprint index (see Sanderson et al., 2002); the other metric introduced by Gumbs et al. (2020) is Terminal Endemism or TE which weights terminal branch length by its range, a similar approach to Jetz et al.'s (2014) Evolutionary Distinctness Rarity. There are also more intraspecific-focused, genetic-based approaches that provide important insight into population level conservation strategies and are the focus of much attention (Beger et al., 2014; Nielsen et al., 2017, 2020).

The novel methodology presented in Chapter 4 has the ability to incorporate other elements important to the conservation of biodiversity, rarity or threat level for example, or even other elements of evolution like endemism. This could be done at the stage in the method where sets of species, representing the same or very similar amounts of PD, need to be selected out for inclusion into the spatial conservation planning element. These other elements could be incorporated to select a set of species that not only maximises PD but that also accounts for other aspects important to the conservation of biodiversity. For example, resulting in a set of species optimally selected to maximise PD that have also been selected after this point to maximise the inclusion of endangered species. Exploration of this would be a useful extension to the work presented in this thesis.

PD was chosen as the sole metric in this study. However, comparisons between different metrics (*e.g.* between PD and functional diversity, or between PD and WEGE), and also between approaches that use the same metric but in different ways - for example, the two different approaches, for incorporating PD into spatial conservation planning, used within this thesis (weighted branch-based and optimised selection of species) - would provide much needed insight into how integrated approaches could most efficiently serve to conserve biodiversity.

Functional diversity has become a valued metric that has garnered recognition alongside the more evolutionary-focussed metrics. Functional diversity classifies each species as an assemblage of traits that determine how these individuals interact with the environment and each other, thus providing an indication of functional role(s) they play within a given ecosystem (McGill et al., 2006). Some authors have argued that PD is able to capture this functional diversity successfully (Faith, 1992; Winter et al., 2013), and this assumption has driven important PD-based metrics such as EDGE (Isaac et al., 2007). However, Mazel et al. (2018) refer to this approach of assuming that PD will capture functional diversity as the "phylogenetic gambit", and these same authors found that prioritising PD for >15,000 vertebrate species across the globe is unreliable at capturing functional diversity. This again highlights the need for more integrated approaches to conservation that recognise the multi-faceted nature of biodiversity; the world is a diverse place that needs varied, case-specific, and objective-led approaches The novel approach to incorporating PD within a spatial conservation plan via the optimised selection of species, presented in Chapter 4, could integrate functional diversity. Functional diversity could be used in the set selection part of the methodology, where the species selected would represent the maximum amount of functional diversity for an already maximised amount of PD, or vice versa, where functional diversity is prioritised initially. A combination metric that accounts for both PD and functional diversity at the same time could also feasibly be developed, but further work is needed, that also takes into account the amount of surrogacy between these two metrics, something that is debated within the literature (see Mazel et al., 2018; Owen et al., 2019).

6.1.7 CONCLUDING REMARKS

PD captures an important element of biodiversity by quantifying the process by which biodiversity came to be and continues to persist - evolution. This body of work represents a continued investigation of the use of PD within conservation and provides an addition to the "toolbox" designed to help integrate PD into effective spatial conservation planning. Biodiversity is multidimensional, and these different dimensions, as captured by PD and functional diversity for example, are unevenly distributed between species. Conservation requires those involved to acknowledge this within their decisions and to move away from species as the sole unit for the conservation of biodiversity, certainly if their aims are to

protect more than just species richness. Indeed, an argument could also be made that if these other dimensions, which are associated with the stability of an ecosystem (Cadotte et al., 2012), are not considered then species richness could also be negatively impacted.
The field of evolutionary focused spatial conservation planning is young, and this work is at the cutting edge. With the need for effective conservation approaches being vitally important in the face of the greatest loss in biodiversity the world has ever seen (WWF, 2020; Ceballos et al., 2017; Pimm & Raven, 2000) the conclusion of this work is a call for more integrated and collaborative conservation efforts that account for the many different, previously under represented, dimensions of biodiversity.

APPENDIX

I.) EVERY TIP PER NODE

Every tip per node will provide an index of every tip, *i.e.* species, that descends from every node within a phylogenetic tree. This index is then used in the ‘get unions from ’every tip per node’’ function:

```
library(phytools)
library(sf)
library(phangorn)

obj = scan('twee310.txt',n=1, what="character") ##sorting format
twee = phytools::read.newick(text=obj) ##reading in file
plot(twee)
twee ##Phylogenetic tree with 310 tips and 309 internal nodes

nodelabels() # check node labels

#define function:

everyTipPerNode <- function(tree){
 # first need to get just the internal node labels
 nodeNos = c((length(tree$tip.label)+1) : (length(tree$tip.label) + tree$N
node))
 nodeNames <- sapply(nodeNos, function(x)paste("node_",sep="",x )) # next
part produces names in ascending order
 # get the index of just the extant descendents (tips) of those nodes
 tipsPerNode = phangorn::Descendants(twee, node = nodeNos, type="tips")
 # get the tip labels (names)
 tipsNamesPerNode = lapply(tipsPerNode, function(x) tree$tip.label[x])
 names(tipsNamesPerNode) = nodeNames
 return(tipsNamesPerNode)
}

# run the function
test = everyTipPerNode(twee)

test

# next step is read in polygon data and assign each polygon to spp. names
as they appear in tree
# then do join of the polygons for all spp in each list element from above
```

II.) GET UNIONS FROM EVERY TIP PER NODE

This function uses the index from ‘every tip per node’ in conjunction with a shapefile containing the range of every species (tip) in the phylogeny and through unioning all the species ranges that descend from each node to create a new spatial range for every branch in the phylogeny, exported as a shapefiles:

```
library(phytools)
library(sf)
library(phangorn)
library(dplyr)
library(rmapshaper)

#read in polygon data and assign each polygon to spp. names as they appear
in tree
# then do join of the polygons for all spp in each list element from above


all.sp<- st_read('IUCN_310sp.shp') %>% select(binomial)
all.sp

# geometry for each node:
getUnions <- function(poly, namesRow, tipNodes) {
 testList = list()
 for (i in 1:length(test)){
  testList[[i]] <- poly %>% dplyr::filter(binomial %in% c(tipNodes[[i]]))
 }
 unions = lapply(testList, function(x)st_combine(x))
 return(unions)
}

xxx = getUnions(all.sp, "binomial", test)
xxx[[301]]

for(i in 1:length(xxx)){
st_write(xxx[[i]], paste0(names(test)[[i]],".shp"), driver="ESRI Shapefile
")
}
```

III.) CREATE MARXAN SPECIES FILE FOR EVERY SET

Writes a bespoke MAXRAN target file (spec.dat) for every set of species at given level of PD, reads in a list of numbered/Id'd species, the output file from PDA optimisation read out, and an existing base target (Spec) file, containing targets. It then creates new Spec files for every optimisation combination from a given K value in pda.exe *i.e.* it alters a base level spec file where every species target is set, in this case 17% of its total range. It sets every species that does NOT appear in the PDA file to 0, it does this for every set of species for that specific K value (number of species):

```
library(magrittr)
library(tidyverse)

names <- read_csv("names_ids_groves115.csv") ##species ID and names file
marx <- readLines("GG_k51_pd80_set117.pda") ##pda.exe output file, contain
ing all species combos for given -K value
spec <- read_tsv("spec_GG_17Prop_RAW.dat") ##spec file from Marxan input -
all species (prim310 for example) with targets set - (e.g. to 17% prop)
spec %<>% dplyr::mutate(species=names$binomial)


chop_head <- 98 # chop to before first line "PD set 1 and covers... ##
marx2 = marx[-c(1:chop_head)] ##getting rid of top portion of pda.exe read
out


##spliting pda.exe into each combo and setting targets to every species th
at doesnt appear in both lists to zero
marx3 = split(marx2, ceiling(seq_along(marx2)/(52+ 1)))
##change larger number here to value of K plus 1. (and then also +1)
marx3 = marx3[-c(length(marx3))]

marx4 = lapply(marx3, function(x) {x[-c(1,length(x))]})

spec_list <- lapply(1:length(marx4), function(x) spec)

for(i in 1:length(spec_list)){
 spec_list[[i]][!spec$species %in% marx4[[i]], 2] <- 0
}

index = c(1:length(spec_list))
for(i in 1:length(spec_list)){
 write.table(spec_list[[i]],file = paste('spec_',length(marx4[[1]]),"_",in
dex[[i]], '.dat',sep=""), sep="\t",row.names = F, quote=F) ####Writes .dat
files used by marxan###
}
```

IV.) MARXAN LOOP FOR SETS

Runs MARXAN in a loop for every set of species for a given level of PD. Sets determined by PDA, target files (species files) created for each set using the ‘Create MARXAN species file for every set’:

```
#Run Marxan with different Target files
#input.dat should be Marxan Folder

# List different Target files
target.files<-list.files("C:/Users/stuart/Desktop/upham/CORE/C3/MARXAN/gro
ves/targets", pattern='spec_')
# Make directory names from them
target.dir<-stringr::str_replace(target.files,"[.].*$","")

##All the target Files - the output from 'optimisation_PDA_create_spec.R'
(e.g.spec_155_1) have to be copied into the input dir.in with pu.dat puvsp
. dat ##

for(i in 1:length(target.files)) {
 target.file<-target.files[i]
 input.file <- dir(path='C:/Users/stuart/Desktop/upham/CORE/C3/MARXAN/grov
es', pattern = "input.dat") #read input.dat
 input <- readLines(input.file, n = -1)
 dir.create(paste("C:/Users/stuart/Desktop/upham/CORE/C3/MARXAN/groves/out
put/", target.dir[i], sep='')) #create output folder for saving results

 #Modify Target file name in Input.dat
 #can modify output file name instead of scenario name preference is to ha
ve marxan output files in different folders
 input[29] <- paste("SPECNAME", target.files[i], sep = " ")
 input[35] <- paste("SCENNAME", target.files[i], sep=" ")
 input[45] <- paste("OUTPUTDIR", paste("C:/Users/stuart/Desktop/upham/CORE
/C3/MARXAN/groves/output/", target.dir[i], sep=""), sep=" ")

 write(input,"input.dat")# Re-write input file at each run with the corres
ponding parameters changed

 #Run Marxan using the target file being used in the loop. Marxan.x64 shou
ld be in the same folder as input.dat and all other files (pu, spvspu and
bound)in the same folder as the target file
 system("Marxan.exe", wait = T, invisible = F) # Call Marxan to execute

}
```

REFERENCES

Agapow, P., Bininda-Emonds, O. R. P., Crandall, K. A., Gittleman, J. L., Mace, G. M., Marshall, J. C., & Purvis, A. (2004). The impact of species concept on biodiversity studies. *The Quarterly Review of Biology*, *79*(2), 161–179. https://doi.org/10.1086/383542

Alagador, D., & Cerdeira, J. O. (2020). Revisiting the minimum set cover, the maximal coverage problems and a maximum benefit area selection problem to make climate-change-concerned conservation plans effective. *Methods in Ecology and Evolution*, *11*(10), 1325–1337. https://doi.org/10.1111/2041-210X.13455

Allan, J. R., Watson, J. E. M., Marco, M. D., O'Bryan, C. J., Possingham, H. P., Atkinson, S. C., & Venter, O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biology*, *17*(3), e3000158. https://doi.org/10.1371/journal.pbio.3000158

Allnutt, T. F., McClanahan, T. R., Andréfouët, S., Baker, M., Lagabrielle, E., McClennen, C., Rakotomanjaka, A. J. M., Tianarisoa, T. F., Watson, R., & Kremen, C. (2012). Comparison of marine spatial planning methods in madagascar demonstrates value of alternative approaches. *PLoS ONE*, *7*(2), e28969. https://doi.org/10.1371/journal.pone.0028969

Almond, R. E. A., Grooten, M., & Petersen, T. (Eds.). (2020). *WWF (2020) Living Planet Report 2020—Bending the curve of biodiversity loss. Living Planet Report 2020—Bending the curve of biodiversity loss*. WWF, Gland, Switzerland

Ardron, J. A., Possingham, H. P., & Klein, C. J. (2010). *Marxan Good Practices Handbook, Version 2*. Pacific Marine Analysis and Research Association. www.pacmara.org.

Arponen, A., & Zupan, L. (2016). Representing hotspots of evolutionary history in systematic conservation planning for European mammals. In R. Pellens & P. Grandcolas (Eds.), *Biodiversity Conservation and Phylogenetic Systematics* (Vol. 14, pp. 265–285). Springer International Publishing. https://doi.org/10.1007/978-3-319-22461-9_13

Ashley, M. V., Willson, M. F., Pergams, O. R. W., O'Dowd, D. J., Gende, S. M., & Brown, J. S. (2003). Evolutionarily enlightened management. *Biological Conservation*, *111*(2), 115–123. https://doi.org/10.1016/S0006-3207(02)00279-3

Asmyhr, M. G., Linke, S., Hose, G., & Nipperess, D. A. (2014). Systematic Conservation Planning for Groundwater Ecosystems Using Phylogenetic Diversity. *PLoS ONE*, *9*(12), e115132. https://doi.org/10.1371/journal.pone.0115132

Ball, I.R. & Possingham, H.P. (2000). *Marxan (v1.8.2): Marine reserve design using spatially explicit annealing, a manual*. University of Queensland, Brisbane, Australia.

Ball, I.R., Possingham, H.P., & Watts, M. (2009). Marxan and relatives: software for spatial conservation prioritisation. In: Moilanen, A., Wilson, K. A., & Possingham, H. P., (eds) *Spatial conservation prioritisation: quantitative methods and computational tools*. Oxford University Press, Oxford

Beger, M., Selkoe, K. A., Treml, E., Barber, P. H., von der Heyden, S., Crandall, E. D., Toonen, R. J., & Riginos, C. (2014). Evolving coral reef conservation with genetic information. *Bulletin of Marine Science*, *90*(1), 159–185. https://doi.org/10.5343/bms.2012.1106

Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L., & Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, *446*(7135), 507–512. https://doi.org/10.1038/nature05634

Bottrill, M. C., & Pressey, R. L. (2012). The effectiveness and evaluation of conservation planning: Evaluation and conservation planning. *Conservation Letters*, *5*(6), 407–420. https://doi.org/10.1111/j.1755-263X.2012.00268.x

Bowen, B. W. (1999). Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Molecular Ecology*, *8*(s1), S5–S10. https://doi.org/10.1046/j.1365-294X.1999.00798.x

Bowler, D. E., Bjorkman, A. D., Dornelas, M., Myers-Smith, I. H., Navarro, L. M., Niamir, A., Supp, S. R., Waldock, C., Winter, M., Vellend, M., Blowes, S. A., Böhning-Gaese, K., Bruelheide, H., Elahi, R., Antão, L. H., Hines, J., Isbell, F., Jones, H. P., Magurran, A. E., … Bates, A. E. (2020). Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature*, *2*(2), 380–394. https://doi.org/10.1002/pan3.10071

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D., & Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58–61. https://doi.org/10.1126/science.1127609

Brum, F. T., Graham, C. H., Costa, G. C., Hedges, S. B., Penone, C., Radeloff, V. C., Rondinini, C., Loyola, R., & Davidson, A. D. (2017). Global priorities for conservation across multiple dimensions of mammalian diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(29), 7641–7646. https://doi.org/10.1073/pnas.1706461114

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Cabeza, M., & Moilanen, A. (2001). Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution*, *16*(5), 242–248. https://doi.org/10.1016/S0169-5347(01)02125-5

Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences*, *110*(22), 8996–9000. https://doi.org/10.1073/pnas.1301685110

Cadotte, M. W., & Davies, T. J. (2010). Rarest of the rare: Advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, *16*(3), 376–385. https://doi.org/10.1111/j.1472-4642.2010.00650.x

Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, *93*(sp8), S223–S233. https://doi.org/10.1890/11-0426.1

Cantalapiedra, J. L., Aze, T., Cadotte, M. W., Dalla Riva, G. V., Huang, D., Mazel, F., Pennell, M. W., Ríos, M., & Mooers, A. Ø. (2019). Conserving evolutionary history does not result in greater diversity over geological time scales. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1904), 20182896. https://doi.org/10.1098/rspb.2018.2896

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Carta, A., Gargano, D., Rossi, G., Bacchetta, G., Fenu, G., Montagnani, C., Abeli, T., Peruzzi, L., & Orsenigo, S. (2019). Phylogenetically informed spatial planning as a tool to prioritise areas for threatened plant conservation within a Mediterranean biodiversity hotspot. *Science of The Total Environment*, *665*, 1046–1052. https://doi.org/10.1016/j.scitotenv.2019.02.127

Carta, A., Pierini, B., Roma-Marzio, F., Bedini, G., & Peruzzi, L. (2018). Phylogenetic measures of biodiversity uncover pteridophyte centres of diversity and hotspots in Tuscany. *Plant Biosystems*, *152*(4), 831–839. https://doi.org/10.1080/11263504.2017.1353550

Carvalho, R. A. de, Vinicius Cianciaruso, M., Trindade-Filho, J., Dalia Sagnori, M., & Dias Loyola, R. (2010). Drafting a blueprint for functional and phylogenetic diversity conservation in the Brazilian Cerrado. *Natureza & Conservação*, *08*(02), 171–176. https://doi.org/10.4322/natcon.00802011

Carvalho, S. B., Velo-Antón, G., Tarroso, P., Portela, A. P., Barata, M., Carranza, S., Moritz, C., & Possingham, H. P. (2017). Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. *Nature Ecology & Evolution*, *1*(6), 0151. https://doi.org/10.1038/s41559-017-0151

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signalled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., & Tilman, D. (1997). Biotic control over the functioning of ecosystems. *Science*, *277*(5325), 500–504. https://doi.org/10.1126/science.277.5325.500

Chernomor, O., Minh, B. Q., Forest, F., Klaere, S., Ingram, T., Henzinger, M., & Haeseler, A. von. (2015). Split diversity in constrained conservation prioritization using integer linear programming. *Methods in Ecology and Evolution*, *6*(1), 83–91. https://doi.org/10.1111/2041-210X.12299

Christenhusz, M. J. M. (2020). On species concepts, phylogenetics and the science of natural history—Three current issues facing taxonomy. *Megataxa*, *1*(1), 67–72. https://doi.org/10.11646/megataxa.1.1.14

Coelho de Souza, F., Dexter, K. G., Phillips, O. L., Pennington, R. T., Neves, D., Sullivan, M. J. P., Alvarez-Davila, E., Alves, Á., Amaral, I., Andrade, A., Aragao, L. E. O. C., Araujo-Murakami, A., Arets, E. J. M. M., Arroyo, L., C, G. A. A., Bánki, O., Baraloto, C., Barroso, J. G., Boot, R. G. A., … Baker, T. R. (2019). Evolutionary diversity is associated with wood productivity in Amazonian forests. *Nature Ecology & Evolution*, *3*(12), 1754–1761. https://doi.org/10.1038/s41559-019-1007-y

Cotterill, F. P. D., Taylor, P. J., Gippoliti, S., Bishop, J. M., & Groves, C. P. (2014). Why one century of phenetics is enough: response to “are there really twice as many bovid species as we thought?” *Systematic Biology*, *63*(5), 819–832. https://doi.org/10.1093/sysbio/syu003

Cowling, R. M., & Pressey, R. L. (2001). Rapid plant diversification: Planning for an evolutionary future. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(10), 5452–5457. https://doi.org/10.1073/pnas.101093498

Cracraft, J. (1983). Species concepts and speciation analysis. In R. F. Johnston (Ed.), *Current Ornithology* (pp. 159–187). Springer, US. https://doi.org/10.1007/978-1-4615-6781-3_6

Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution*, *15*(7), 290–295. https://doi.org/10.1016/S0169-5347(00)01876-0

Crozier, R. H. (1992). Genetic diversity and the agony of choice. *Biological Conservation*, *61*(1), 11–15. https://doi.org/10.1016/0006-3207(92)91202-4

Crozier, R. H. (1997). Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. *Annual Review of Ecology and Systematics*, *28*(1), 243–268. https://doi.org/10.1146/annurev.ecolsys.28.1.243

Daru, B. H., le Roux, P. C., Gopalraj, J., Park, D. S., Holt, B. G., & Greve, M. (2019). Spatial overlaps between the global protected areas network and terrestrial hotspots of evolutionary diversity. *Global Ecology and Biogeography*, *28*(6), 757–766. https://doi.org/10.1111/geb.12888

del Hoyo, J., & Collar, N. J. (2014). *Illustrated checklist of the birds of the World* (Vol. 1). Lynx Edicions.

del Hoyo, J., & Collar, N. J. (2016). *Illustrated checklist of the birds of the world* (Vol. 2). Lynx Edicions.

Delavenne, J., Metcalfe, K., Smith, R. J., Vaz, S., Martin, C. S., Dupuis, L., Coppin, F., & Carpentier, A. (2012). Systematic conservation planning in the eastern English Channel: Comparing the Marxan and Zonation decision-support tools. *ICES Journal of Marine Science*, *69*(1), 75–83. https://doi.org/10.1093/icesjms/fsr180

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world: Spatial mismatch between diversity facets. *Ecology Letters*, no-no. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Diniz-Filho, J. A. F., Loyola, R. D., Raia, P., Mooers, A. O., & Bini, L. M. (2013). Darwinian shortfalls in biodiversity conservation. *Trends in Ecology & Evolution*, *28*(12), 689–695. https://doi.org/10.1016/j.tree.2013.09.003

Diniz-Filho, J. A. F., & Bini, L. M. (2011). Geographical Patterns in Biodiversity: Towards an Integration of Concepts and Methods from Genes to Species Diversity. *Natureza & Conservação*, *9*(2), 179–187. https://doi.org/10.4322/natcon.2011.023

Domínguez Lozano, F., Moreno Saiz, J. C., Sainz Ollero, H., & Schwartz, M. W. (2007). Effects of dynamic taxonomy on rare species and conservation listing: Insights from the Iberian vascular flora. *Biodiversity and Conservation*, *16*(14), 4039–4050. https://doi.org/10.1007/s10531-007-9206-2

dos Reis, M., Gunnell, G. F., Barba-Montoya, J., Wilkins, A., Yang, Z., & Yoder, A. D. (2018). Using phylogenomic data to explore the effects of relaxed clocks and calibration strategies on divergence time estimation: Primates as a test case. *Systematic Biology*, *67*(4), 594–615. https://doi.org/10.1093/sysbio/syy001

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Faith, D. P. (1996). Conservation priorities and phylogenetic pattern. *Conservation Biology*, *10*(4), 1286–1289. https://doi.org/10.1046/j.1523-1739.1996.10041286.x

Faith, D. P. (2002). Quantifying biodiversity: a phylogenetic perspective. *Conservation Biology*, *16*(1), 248–252. https://doi.org/10.1046/j.1523-1739.2002.00503.x

Faith, D. P. (2008). Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. *Conservation Biology*, *22*(6), 1461–1470. https://doi.org/10.1111/j.1523-1739.2008.01068.x

Faith, D. P. (2015). Phylogenetic diversity, functional trait diversity and extinction: Avoiding tipping points and worst-case losses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1662), 20140011. https://doi.org/10.1098/rstb.2014.0011

Faith, D. P. (2019). EDGE of existence and phylogenetic diversity. *Animal Conservation*, *22*(6), 537–538. https://doi.org/10.1111/acv.12552

Farooq, H., Azevedo, J., Belluardo, F., Nanvonamuquitxo, C., Bennett, D., Moat, J., Soares, A., Faurby, S., & Antonelli, A. (2020). WEGE: A new metric for ranking locations for biodiversity conservation. *Diversity and Distributions*, *26*(11), 1456–1466. https://doi.org/10.1111/ddi.13148

Faurby, S., & Svenning, J.-C. (2015). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, *21*(10), 1155–1166. https://doi.org/10.1111/ddi.12369

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection.* Oxford University Press, Oxford

Forest, F., Grenyer, R., Rouget, M., Davies, T. J., Cowling, R. M., Faith, D. P., Balmford, A., Manning, J. C., Procheş, Ş., van der Bank, M., Reeves, G., Hedderson, T. A. J., & Savolainen, V. (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, *445*(7129), 757–760. https://doi.org/10.1038/nature05587

Fox, N. J., & Beckley, L. E. (2005). Priority areas for conservation of Western Australian coastal fishes: A comparison of hotspot, biogeographical and complementarity approaches. *Biological Conservation*, *125*(4), 399–410. https://doi.org/10.1016/j.biocon.2005.02.006

Frankham, R., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C., Mendelson, J. R., Porton, I. J., Ralls, K., & Ryder, O. A. (2012). Implications of different species concepts for conserving biodiversity. *Biological Conservation*, *153*, 25–31. https://doi.org/10.1016/j.biocon.2012.04.034

Fritz, S. A., & Purvis, A. (2010). Phylogenetic diversity does not capture body size variation at risk in the world’s mammals. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1693), 2435–2441. https://doi.org/10.1098/rspb.2010.0030

Garnett, S. T., Crowley, G. M., & Stattersfield, A. J. (2003). Changes in the conservation status of Australian birds resulting from differences in taxonomy, knowledge and the definitions of threat. *Biological Conservation*, *113*(2), 269–276. https://doi.org/10.1016/S0006-3207(02)00377-4

Garnett, S. T., & Christidis, L. (2017). Taxonomy anarchy hampers conservation. *Nature*, *546*(7656), 25–27. https://doi.org/10.1038/546025a

Garnett, S. T., Christidis, L., Conix, S., Costello, M. J., Zachos, F. E., Bánki, O. S., Bao, Y., Barik, S. K., Buckeridge, J. S., Hobern, D., Lien, A., Montgomery, N., Nikolaeva, S., Pyle, R. L., Thomson, S. A., Dijk, P. P. van, Whalen, A., Zhang, Z.-Q., & Thiele, K. R. (2020). Principles for creating a single authoritative list of the world's species. *PLoS Biology*, *18*(7), e3000736. https://doi.org/10.1371/journal.pbio.3000736

Gippoliti, S. (2019). Species delimitation in mammals: A comment on Zachos (2018). *Mammalian Biology*, *94*, 127–131. https://doi.org/10.1016/j.mambio.2018.05.007

Gippoliti, S., Cotterill, F. P. D., & Groves, C. P. (2013). Mammal taxonomy without taxonomists: A reply to Zachos and Lovari. *Hystrix*, *24*(2), 145–147. https://doi.org/10.4404/hystrix-24.1-8881

Gippoliti, S., Cotterill, F. P. D., Zinner, D., & Groves, C. P. (2018). Impacts of taxonomic inertia for the conservation of African ungulate diversity: An overview: Taxonomic inertia and ungulate conservation. *Biological Reviews*, *93*(1), 115–130. https://doi.org/10.1111/brv.12335

Gippoliti, S., & Groves, C. P. (2013). 'Taxonomic inflation' in the historical context of mammalogy and conservation. *Hystrix*, *23*(2), 8–11. https://doi.org/10.4404/hystrix-23.2-8685

Gippoliti, S., & Groves, C. P. (2018). Overlooked mammal diversity and conservation priorities in Italy: Impacts of taxonomic neglect on a Biodiversity Hotspot in Europe. *Zootaxa*, *4434*(3), 511–528. https://doi.org/10.11646/zootaxa.4434.3.7

Groves, C. (2001). Why taxonomic stability is a bad idea, or why are there so few species of primates (or are there?). *Evolutionary Anthropology: Issues, News, and Reviews*, *10*(6), 192–198. https://doi.org/10.1002/evan.10005

Groves, C., & Grubb, P. (2011). *Ungulate Taxonomy*. The Johns Hopkins University Press, Baltimore, US

Groves, C. P. (2013). The nature of species: A rejoinder to Zachos et al. *Mammalian Biology*, *78*(1), 7–9. https://doi.org/10.1016/j.mambio.2012.09.009

Gumbs, R., Gray, C. L., Böhm, M., Hoffmann, M., Grenyer, R., Jetz, W., Meiri, S., Roll, U., Owen, N. R., & Rosindell, J. (2020). Global priorities for conservation of reptilian phylogenetic diversity in the face of human impacts. *Nature Communications*, *11*(1), 2616. https://doi.org/10.1038/s41467-020-16410-6

Gumbs, R., Gray, C. L., Wearn, O. R., & Owen, N. R. (2018). Tetrapods on the EDGE: Overcoming data limitations to identify phylogenetic conservation priorities. *PLoS ONE*, *13*(4), e0194680. https://doi.org/10.1371/journal.pone.0194680

Heller, R., Frandsen, P., Lorenzen, E. D., & Siegismund, H. R. (2013). Are there really twice as many bovid species as we thought? *Systematic Biology*, *62*(3), 490–493. https://doi.org/10.1093/sysbio/syt004

Henriques, R., Mann, B. Q., Nielsen, E. S., Hui, C., & Heyden, S. von der. (2020). Extending biodiversity conservation with functional and evolutionary diversity: A case study of South African sparid fishes. *African Journal of Marine Science*, *0*(0), 1–7. https://doi.org/10.2989/1814232X.2020.1798282

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K., Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A. S. L., Tognelli, M. F., … Stuart, S. N. (2010). The impact of conservation on the status of the world’s vertebrates. *Science*, *330*(6010), 1503–1509. https://doi.org/10.1126/science.1194442

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, *11*(6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

ILOG. (1999). *C-PLEX* (6.5) [Computer software]. https://www.rpi.edu/dept/math/math-programming/cplex66/sun4x_56/doc/relnotes65/onlinedoc/index.html

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES. (2018). *The IPBES regional assessment report on biodiversity and ecosystem services for Asia and the Pacific* (Report). Zenodo. https://doi.org/10.5281/ZENODO.3237373

Isaac, N. J. B., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: Its influence on macroecology and conservation. *Trends in Ecology & Evolution*, *19*(9), 464–469. https://doi.org/10.1016/j.tree.2004.06.004

Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C., & Baillie, J. E. M. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE*, *2*(3), e296. https://doi.org/10.1371/journal.pone.0000296

The International Union for Conservation of Nature (IUCN). (2016). *A Global Standard for the Identification of Key Biodiversity Areas, Version 1.0.* IUCN. Gland, Switzerland

The International Union for Conservation of Nature (IUCN). (2019). *Spatial data download - Terrestrial mammals.* Retrieved October 19, 2019, from https://www.iucnredlist.org/resources/spatial-data-download

Jenkins, C. N., & Joppa, L. (2009). Expansion of the global terrestrial protected area system. *Biological Conservation*, *142*(10), 2166–2174. https://doi.org/10.1016/j.biocon.2009.04.016

Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology & Evolution*, *2*(5), 850–858. https://doi.org/10.1038/s41559-018-0515-5

Jetz, W., Thomas, G. H., Joy, J. B., Redding, D. W., Hartmann, K., & Mooers, A. O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, *24*(9), 919–930. https://doi.org/10.1016/j.cub.2014.03.011

Klein, C., Wilson, K., Watts, M., Stein, J., Berry, S., Carwardine, J., Smith, M. S., Mackey, B., & Possingham, H. (2009). Incorporating ecological and evolutionary processes into continental-scale conservation planning. *Ecological Applications*, *19*(1), 206–217.

Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W., & Shugart, H. H. (2006). Global tests of biodiversity concordance and the importance of endemism. *Nature*, *440*(7081), 212–214. https://doi.org/10.1038/nature04291

Lindegren, M., Holt, B. G., MacKenzie, B. R., & Rahbek, C. (2018). A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Scientific Reports*, *8*(1), 4099. https://doi.org/10.1038/s41598-018-22419-1

Mace, G. M. (2004). The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*(1444), 711–719. https://doi.org/10.1098/rstb.2003.1454

Maddison, W. P., & Maddison, D. R. (2019). *Mesquite: A modular system for evolutionary analysis* (3.61) [Computer software]. http://www.mesquiteproject.org

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405*(11), 243–253. https://doi.org/10.1038/35012251

Marshall, A. J., & Wich, S. A. (2016). Why conserve primates? In S. A. Wich & A. J. Marshall (Eds.), *An Introduction to Primate Conservation* (pp. 13–30). Oxford University Press, Oxford. https://doi.org/10.1093/acprof:oso/9780198703389.003.0002

Mayr, E. (1943). Systematics and the origin of species. *Annals of the Entomological Society of America*, *36*(1), 138–139. https://doi.org/10.1093/aesa/36.1.138a

Mazel, F., Pennell, M. W., Cadotte, M. W., Diaz, S., Dalla Riva, G. V., Grenyer, R., Leprieur, F., Mooers, A. O., Mouillot, D., Tucker, C. M., & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications*, *9*(1), 2888. https://doi.org/10.1038/s41467-018-05126-3

Mazel, F., Renaud, J., Guilhaumon, F., Mouillot, D., Gravel, D., & Thuiller, W. (2015). Mammalian phylogenetic diversity-area relationships at a continental scale. *Ecology*, *96*(10), 2814–2822. https://doi.org/10.1890/14-1858.1

McCarthy, D. P., Donald, P. F., Scharlemann, J. P. W., Buchanan, G. M., Balmford, A., Green, J. M. H., Bennun, L. A., Burgess, N. D., Fishpool, L. D. C., Garnett, S. T., Leonard, D. L., Maloney, R. F., Morling, P., Schaefer, H. M., Symes, A., Wiedenfeld, D. A., & Butchart, S. H. M. (2012). Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. *Science*, *338*(6109), 946–949. https://doi.org/10.1126/science.1229803

McClure, C. J. W., Lepage, D., Dunn, L., Anderson, D. L., Schulwitz, S. E., Camacho, L., Robinson, B. W., Christidis, L., Schulenberg, T. S., Iliff, M. J., Rasmussen, P. C., & Johnson, J. (2020). Towards reconciliation of the four world bird lists: Hotspots of disagreement in taxonomy of raptors. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1929), 20200683. https://doi.org/10.1098/rspb.2020.0683

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McNeely, A., Miller, K. R., Reid, W. V., Mittermeier, R. A., & Werner, T. B. (1990). Strategies for conserving biodiversity. *Environment: Science and Policy for Sustainable Development*, *32*(3), 16–40. https://doi.org/10.1080/00139157.1990.9929017

Meijaard, E., & Rawson, B. (2015). The phylogenetic species concept and its role in Southeast Asian mammal conservation. In A. M. Behie & M. F. Oxenham (Eds.), *Taxonomic Tapestries: The Threads of Evolutionary, Behavioural and Conservation Research*. ANU Press. https://doi.org/10.22459/TT.05.2015.16

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. *Biological Conservation*, *134*(4), 571–579. https://doi.org/10.1016/j.biocon.2006.09.008

Moilanen, A., Franco, A. M. A., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. (2005). Prioritizing multiple-use landscapes for conservation: Methods for large multi-species planning problems. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1575), 1885–1891. https://doi.org/10.1098/rspb.2005.3164

Moilanen, A., Meller, L., Leppänen, J., Pouzols, F. M., Kujala, H., & Arponen, A. (2012). *Zonation Spatial Conservation Planning Framework and Sofware V3.1, [User Manual]*. Edita, Helsinki

Moritz, C. (2002). Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, *51*(2), 238–254. https://doi.org/10.1080/10635150252899752

Morrison, W. R., Lohr, J. L., Duchen, P., Wilches, R., Trujillo, D., Mair, M., & Renner, S. S. (2009). The impact of taxonomic change on conservation: Does it kill, can it save, or is it just irrelevant? *Biological Conservation*, *142*(12), 3201–3206. https://doi.org/10.1016/j.biocon.2009.07.019

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nielsen, E. S., Beger, M., Henriques, R., Selkoe, K. A., & von der Heyden, S. (2017). Multispecies genetic objectives in spatial conservation planning: Multispecies Genetic Planning. *Conservation Biology*, *31*(4), 872–882. https://doi.org/10.1111/cobi.12875

Nielsen, E. S., Beger, M., Henriques, R., & von der Heyden, S. (2020). A comparison of genetic and genomic approaches to represent evolutionary potential in conservation planning. *Biological Conservation*, *251*, 108770. https://doi.org/10.1016/j.biocon.2020.108770

Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, *4*(4), 355–364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x

Okoli, C. (2015). A guide to conducting a standalone systematic literature review. *Communications of the Association for Information Systems*, *37*(1). https://doi.org/10.17705/1CAIS.03743

Olivieri, I., Tonnabel, J., Ronce, O., & Mignot, A. (2016). Why evolution matters for species conservation: Perspectives from three case studies of plant metapopulations. *Evolutionary Applications*, *9*(1), 196–211. https://doi.org/10.1111/eva.12336

Owen, N. R., Gumbs, R., Gray, C. L., & Faith, D. P. (2019). Global conservation of phylogenetic diversity captures more than just functional diversity. *Nature Communications*, *10*(1), 859. https://doi.org/10.1038/s41467-019-08600-8

Pardo, I., Roquet, C., Lavergne, S., Olesen, J. M., Gómez, D., & García, M. B. (2017). Spatial congruence between taxonomic, phylogenetic and functional hotspots: True pattern or methodological artefact? *Diversity and Distributions*, *23*(2), 209–220. https://doi.org/10.1111/ddi.12511

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*(6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., Davis, M., Svenning, J.-C., & Griffin, J. N. (2020). Functional diversity of marine megafauna in the Anthropocene. *Science Advances*, *6*(16), eaay7650. https://doi.org/10.1126/sciadv.aay7650

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752–1246752. https://doi.org/10.1126/science.1246752

Pimm, S. L., & Raven, P. H. (2000). Extinction by numbers. *Nature*, *403*(6772), 843–845. https://doi.org/10.1038/35002708

Polasky, S., Csuti, B., Vossler, C. A., & Meyers, S. M. (2001). A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. *Biological Conservation*, *97*(1), 99–105. https://doi.org/10.1016/S0006-3207(00)00103-8

Pollock, L. J., O'Connor, L. M., Mokany, K., Rosauer, D. F., Talluto, M. V., & Thuiller, W. (2020) Protecting Biodiversity (in all its complexity): New models and methods. *Trends in Ecology & Evolution*, *35*: 1119–1128. https://doi.org/10.1016/j.tree.2020.08.015

Pollock, L. J., Rosauer, D. F., Thornhill, A. H., Kujala, H., Crisp, M. D., Miller, J. T., & McCarthy, M. A. (2015). Phylogenetic diversity meets conservation policy: Small areas are key to preserving eucalypt lineages. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1662), 20140007. https://doi.org/10.1098/rstb.2014.0007

Pollock, L. J., Thuiller, W., & Jetz, W. (2017). Large conservation gains possible for global biodiversity facets. *Nature*, *546*(7656), 141–144. https://doi.org/10.1038/nature22368

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution*, *22*(11), 583–592. https://doi.org/10.1016/j.tree.2007.10.001

Pressey, R. L., Cowling, R. M., & Rouget, M. (2003). Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation*, *112*(1), 99–127. https://doi.org/10.1016/S0006-3207(02)00424-X

Pressey, R. L., Possingham, H. P., & Day, J. R. (1997). Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation*, *80*(2), 207–219. https://doi.org/10.1016/S0006-3207(96)00045-6

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, *526*(7574), 569–573. https://doi.org/10.1038/nature15697

Purvis, A., Agapow, P. M., Gittleman, J. L., & Mace, G. M. (2000). Nonrandom extinction and the loss of evolutionary history. *Science*, *288*(5464), 328–330. https://doi.org/10.1126/science.288.5464.328

Quan, Q., Che, X., Wu, Y., Wu, Y., Zhang, Q., Zhang, M., & Zou, F. (2018). Effectiveness of protected areas for vertebrates based on taxonomic and phylogenetic diversity: Conservation and Phylogenetic Diversity. *Conservation Biology*, *32*(2), 355–365. https://doi.org/10.1111/cobi.12986

Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography*, *18*(2), 200–205.

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, *21*(1), 24–43. https://doi.org/10.1016/0040-5809(82)90004-1

Rapacciuolo, G., Graham, C. H., Marin, J., Behm, J. E., Costa, G. C., Hedges, S. B., Helmus, M. R., Radeloff, V. C., Young, B. E., & Brooks, T. M. (2019). Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. *Nature Ecology & Evolution*, *3*(1), 53–61. https://doi.org/10.1038/s41559-018-0744-7

Ribeiro, B. R., Brum, F. T., Pressey, R. L., & Loyola, R. (2017). Scoring methods do not provide reliable conservation priorities for marine biodiversity protection. *Biological Conservation*, *210*, 349–350. https://doi.org/10.1016/j.biocon.2017.02.038

Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., da Fonseca, G. A. B., Gaston, K. J., Hoffmann, M., Long, J. S., Marquet, P. A., Pilgrim, J. D., Pressey, R. L., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., … Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*(6983), 640–643. https://doi.org/10.1038/nature02422

Rodrigues, A. S. L., & Brooks, T. M. (2007). Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 713–737. https://doi.org/10.1146/annurev.ecolsys.38.091206.095737

Rodrigues, A. S. L., & Gaston, K. J. (2002). Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation*, *105*(1), 103–111. https://doi.org/10.1016/S0006-3207(01)00208-7

Rodrigues, A. S. L., Grenyer, R., Baillie, J. E. M., Bininda-Emonds, O. R. P., Gittlemann, J. L., Hoffmann, M., Safi, K., Schipper, J., Stuart, S. N., & Brooks, T. (2011). Complete, accurate, mammalian phylogenies aid conservation planning, but not much. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2652–2660. https://doi.org/10.1098/rstb.2011.0104

Rosauer, D. F., Blom, M. P. K., Bourke, G., Catalano, S., Donnellan, S., Gillespie, G., Mulder, E., Oliver, P. M., Potter, S., Pratt, R. C., Rabosky, D. L., Skipwith, P. L., & Moritz, C. (2016). Phylogeography, hotspots and conservation priorities: An example from the Top End of Australia. *Biological Conservation*, *204*, 83–93. https://doi.org/10.1016/j.biocon.2016.05.002

Rosauer, D. F., Byrne, M., Blom, M. P. K., Coates, D. J., Donnellan, S., Doughty, P., Keogh, J. S., Kinloch, J., Laver, R. J., Myers, C., Oliver, P. M., Potter, S., Rabosky, D. L., Afonso Silva, A. C., Smith, J., & Moritz, C. (2018). Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy. *Conservation Letters*, *11*(4), e12438. https://doi.org/10.1111/conl.12438

Rosauer, D. F., Laffan, S. W., Crisp, M. D., Donnellan, S. C., & Cook, L. G. (2009). Phylogenetic endemism: A new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, *18*(19), 4061–4072. https://doi.org/10.1111/j.1365-294X.2009.04311.x

Rosauer, D. F., Pollock, L. J., Linke, S., & Jetz, W. (2017). Phylogenetically informed spatial planning is required to conserve the mammalian tree of life. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1865), 20170627. https://doi.org/10.1098/rspb.2017.0627

Sala, O. E., Chapin, F. S., Iii, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sandbrook, C., Fisher, J. A., Holmes, G., Luque-Lora, R., & Keane, A. (2019). The global conservation movement is diverse but not divided. *Nature Sustainability*, *2*(4), 316–323. https://doi.org/10.1038/s41893-019-0267-5

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, *52*(10), 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Santamaría, L., & Méndez, P. F. (2012). Evolution in biodiversity policy - current gaps and future needs: Evolution in biodiversity policy. *Evolutionary Applications*, *5*(2), 202–218. https://doi.org/10.1111/j.1752-4571.2011.00229.x

Scherson, R. A., & Faith, D. P. (Eds.). (2018). *Phylogenetic Diversity: Applications and Challenges in Biodiversity Science*. Springer International Publishing, Basel, Switzerland. https://doi.org/10.1007/978-3-319-93145-6

Sechrest, W., Brooks, T. M., Fonseca, G. A. B. da, Konstant, W. R., Mittermeier, R. A., Purvis, A., Rylands, A. B., & Gittleman, J. L. (2002). Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences*, *99*(4), 2067–2071. https://doi.org/10.1073/pnas.251680798

Shrestha, N., & Wang, Z. (2018). Selecting priority areas for systematic conservation of Chinese Rhododendron: Hotspot versus complementarity approaches. *Biodiversity and Conservation*, *27*(14), 3759–3775. https://doi.org/10.1007/s10531-018-1625-8

Sibarani, M. C., Marco, M. D., Rondinini, C., & Kark, S. (2019). Measuring the surrogacy potential of charismatic megafauna species across taxonomic, phylogenetic and functional diversity on a megadiverse island. *Journal of Applied Ecology*, *56*(5), 1220–1231. https://doi.org/10.1111/1365-2664.13360

Simeonova, V., Bouwma, I., van der Grift, E., Sunyer, C., Manteiga Mart Külvik, L., Suškevičs, M., Dimitrov, S., & Dimitrova, A. (2017). *Natura 2000 and Spatial Planning. Final report for the European Commission. (DG ENV) (Project 07.0202/2015/716477/ETU/ENV. B.3)*. Natura 2000 and Spatial Planning. https://data.europa.eu/doi/10.2779/2947

Simkins, A. T., Buchanan, G. M., Davies, R. G., & Donald, P. F. (2019). The implications for conservation of a major taxonomic revision of the world’s birds. *Animal Conservation*, acv.12545. https://doi.org/10.1111/acv.12545

Sobral, F. L., Jardim, L., Lemes, P., Machado, N., Loyola, R., & Cianciaruso, M. V. (2014). Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. *Natureza & Conservação*, *12*(2), 150–155. https://doi.org/10.1016/j.ncon.2014.09.008

Spalding, M. D., Fish, L., & Wood, L. J. (2008). Toward representative protection of the world's coasts and oceans—progress, gaps, and opportunities. *Conservation Letters*, *1*(5), 217–226. https://doi.org/10.1111/j.1755-263X.2008.00030.x

Springer, M. S., Meredith, R. W., Gatesy, J., Emerling, C. A., Park, J., Rabosky, D. L., Stadler, T., Steiner, C., Ryder, O. A., Janečka, J. E., Fisher, C. A., & Murphy, W. J. (2012). Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLoS ONE*, *7*(11), e49521. https://doi.org/10.1371/journal.pone.0049521

Stillman, J. H. (2003). Acclimation capacity underlies susceptibility to climate change. *Science*, *301*(5629), 65. https://doi.org/10.1126/science.1083073

Strecker, A. L., Olden, J. D., Whittler, J. B., & Paukert, C. P. (2011). Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecological Applications*, *21*(8), 3002–3013.

Sutherland, W. J., Bardsley, S., Bennun, L., Clout, M., Côté, I. M., Depledge, M. H., Dicks, L. V., Dobson, A. P., Fellman, L., Fleishman, E., Gibbons, D. W., Impey, A. J., Lawton, J. H., Lickorish, F., Lindenmayer, D. B., Lovejoy, T. E., Nally, R. M., Madgwick, J., Peck, L. S., … Watkinson, A. R. (2011). Horizon scan of global conservation issues for 2011. *Trends in Ecology & Evolution*, *26*(1), 10–16. https://doi.org/10.1016/j.tree.2010.11.002

Sutherland, W. J., Barnard, P., Broad, S., Clout, M., Connor, B., Côté, I. M., Dicks, L. V., Doran, H., Entwistle, A. C., Fleishman, E., Fox, M., Gaston, K. J., Gibbons, D. W., Jiang, Z., Keim, B., Lickorish, F. A., Markillie, P., Monk, K. A., Pearce-Higgins, J. W., … Ockendon, N. (2017). A 2017 horizon scan of emerging issues for global conservation and biological diversity. *Trends in Ecology & Evolution*, *32*(1), 31–40. https://doi.org/10.1016/j.tree.2016.11.005

Taylor, P. J., Denys, C., & Cotterill, F. P. D. (Woody). (2019). Taxonomic anarchy or an inconvenient truth for conservation? Accelerated species discovery reveals evolutionary patterns and heightened extinction threat in Afro-Malagasy small mammals. *Mammalia*, *83*(4), 313–329. https://doi.org/10.1515/mammalia-2018-0031

Thomson, S. A., Pyle, R. L., Ahyong, S. T., Alonso-Zarazaga, M., Ammirati, J., Araya, J. F., Ascher, J. S., Audisio, T. L., Azevedo-Santos, V. M., Bailly, N., Baker, W. J., Balke, M., Barclay, M. V. L., Barrett, R. L., Benine, R. C., Bickerstaff, J. R. M., Bouchard, P., Bour, R., Bourgoin, T., … Zhou, H.-Z. (2018). Taxonomy based on science is necessary for global conservation. *PLoS Biology*, *16*(3), e2005075. https://doi.org/10.1371/journal.pbio.2005075

Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G. F., Lavergne, S., Renaud, J., Roquet, C., & Mouillot, D. (2015). Conserving the functional and phylogenetic trees of life of European tetrapods. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1662). https://doi.org/10.1098/rstb.2014.0005

Tucker, C. M., Aze, T., Cadotte, M. W., Cantalapiedra, J. L., Chisholm, C., Díaz, S., Grenyer, R., Huang, D., Mazel, F., Pearse, W. D., Pennell, M. W., Winter, M., & Mooers, A. O. (2019). Assessing the utility of conserving evolutionary history. *Biological Reviews*, *94*(5), 1740–1760. https://doi.org/10.1111/brv.12526

Tucker, C. M., Cadotte, M. W., Davies, T. J., & Rebelo, T. G. (2012). Incorporating geographical and evolutionary rarity into conservation prioritization: conservation prioritization. *Conservation Biology*, *26*(4), 593–601. https://doi.org/10.1111/j.1523-1739.2012.01845.x

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological Conservation*, *55*(3), 235–254. https://doi.org/10.1016/0006-3207(91)90030-D

Vasconcelos, R., Brito, J. C., Carvalho, S. B., Carranza, S., & James Harris, D. (2012). Identifying priority areas for island endemics using genetic versus specific diversity – The case of terrestrial reptiles of the Cape Verde Islands. *Biological Conservation*, *153*, 276–286. https://doi.org/10.1016/j.biocon.2012.04.020

Veach, V., Di Minin, E., Pouzols, F. M., & Moilanen, A. (2017). Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. *Diversity and Distributions*, *23*(7), 715–726. https://doi.org/10.1111/ddi.12571

Venter, O., Fuller, R. A., Segan, D. B., Carwardine, J., Brooks, T., Butchart, S. H. M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H. P., Rondinini, C., Smith, R. J., Venter, M., & Watson, J. E. M. (2014). Targeting global protected area expansion for imperiled biodiversity. *PLoS Biology*, *12*(6), e1001891. https://doi.org/10.1371/journal.pbio.1001891

Visconti, P., Butchart, S. H. M., Brooks, T. M., Langhammer, P. F., Marnewick, D., Vergara, S., Yanosky, A., & Watson, J. E. M. (2019). Protected area targets post-2020. *Science*, *364*(6437), eaav6886. https://doi.org/10.1126/science.aav6886

Waldron, A., Mooers, A. O., Miller, D. C., Nibbelink, N., Redding, D., Kuhn, T. S., Roberts, J. T., & Gittleman, J. L. (2013). Targeting global conservation funding to limit immediate biodiversity declines. *Proceedings of the National Academy of Sciences*, *110*(29), 12144–12148. https://doi.org/10.1073/pnas.1221370110

Waples, R. S., Punt, A. E., & Cope, J. M. (2008). Integrating genetic data into management of marine resources: How can we do it better? *Fish and Fisheries*, *9*(4), 423–449. https://doi.org/10.1111/j.1467-2979.2008.00303.x

Watts, M. E., Stewart, R. R., Martin, T. G., Klein, C. J., Carwardine, J., & Possingham, H. P. (2017). Systematic conservation planning with Marxan. In S. E. Gergel & M. G. Turner (Eds.), *Learning Landscape Ecology: A Practical Guide to Concepts and Techniques* (pp. 211–227). Springer, Basel, Switzerland. https://doi.org/10.1007/978-1-4939-6374-4_13

Wicke, K., Mooers, A., & Steel, M. (2020). Formal links between feature diversity and phylogenetic diversity. *BioRxiv*, 2020.04.06.027953. https://doi.org/10.1101/2020.04.06.027953

Wilkins, J. S. (2009). *Species: A history of the idea*. University of California Press, US

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution*, *28*(4), 199–204. https://doi.org/10.1016/j.tree.2012.10.015

Wong, J. S. Y., Chan, Y. K. S., Ng, C. S. L., Tun, K. P. P., Darling, E. S., & Huang, D. (2018). Comparing patterns of taxonomic, functional and phylogenetic diversity in reef coral communities. *Coral Reefs*, *37*(3), 737–750. https://doi.org/10.1007/s00338-018-1698-6

Zachos, F. E. (2015). Taxonomic inflation, the Phylogenetic Species Concept and lineages in the Tree of Life—A cautionary comment on species splitting. *Journal of Zoological Systematics and Evolutionary Research*, *53*(2), 180–184. https://doi.org/10.1111/jzs.12088

Zachos, F. E. (2016). *Species Concepts in Biology. Historical Development, Theoretical Foundations and Practical Relevance*. Springer International Publishing, Basel, Switzerland. https://doi.org/10.1007/978-3-319-44966-1_2

Zachos, F. E. (2018). Mammals and meaningful taxonomic units: The debate about species concepts and conservation. *Mammal Review*, *48*(3), 153–159. https://doi.org/10.1111/mam.12121

Zachos, F. E. (2019). Species delimitation in mammals: A response to Gippoliti. *Mammalian Biology*, *94*, 132–133. https://doi.org/10.1016/j.mambio.2018.05.008

Zachos, F. E., Apollonio, M., Bärmann, E. V., Festa-Bianchet, M., Göhlich, U., Habel, J. C., Haring, E., Kruckenhauser, L., Lovari, S., McDevitt, A. D., Pertoldi, C., Rössner, G. E., Sánchez-Villagra, M. R., Scandura, M., & Suchentrunk, F. (2013). Species inflation and taxonomic artefacts—A critical comment on recent trends in mammalian classification. *Mammalian Biology*, *78*(1), 1–6. https://doi.org/10.1016/j.mambio.2012.07.083

Zachos, F. E., & Lovari, S. (2013). Taxonomic inflation and the poverty of the Phylogenetic Species Concept – a reply to Gippoliti and Groves. *Hystrix, 24*(2), 142–144. https://doi.org/10.4404/hystrix-24.1-8849

Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N., Renaud, J., & Thuiller, W. (2014). Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Diversity and Distributions*, *20*(6), 674–685. https://doi.org/10.1111/ddi.12186