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DOCTORAL THESIS

**Learning from the past to restore trophic complexity
with carnivorous mammals in the Anthropocene**

*A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy*

in the

Division of Evolution, Behaviour and Environment

School of Life Sciences

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22nd September 2021

Declaration

This thesis is a product of my own work during my time at the University of Sussex where I have led the conception, analysis, and writing of all chapters. The thesis conforms to an ‘article format’ in which Chapters 2-6 consist of discrete articles written in styles that are appropriate for publication in peer-reviewed journals in ecology and conservation. Chapters 1 and 7 provide a general introduction to the field and a general discussion.

Chapter 2 is [published](#) in *Proceedings of the Royal Society B* as: Middleton, O. S., J. P. W. Scharlemann, and C. J. Sandom. (2020). “Homogenisation of carnivorous mammal ensembles caused by global range reductions of large-bodied hypercarnivores during the late Quaternary”. *Proceedings of the Royal Society B: Biological Sciences*. 287: 20200804.

The author contributions are: OSM collated data, performed analyses and wrote the first article draft. OSM, CJS, and JPWS contributed to the conception and development of analyses, interpretation of data and manuscript revision.

Chapter 3 is written in the style of an article appropriate for *Ecography* as: Middleton, O. S., J. P. W. Scharlemann, C. J. Sandom. “Lost hypercarnivore functions could be partially reversed on most continents if predators are allowed to recolonise”. *Ecography*.

The author contributions are: OSM led the conception of the article, data collation, analysis, and results interpretation. All authors contributed equally to revising the final article.

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The database can be accessed [here](#) or explored interactively [here](#).

The author contributions are: All authors contributed equally to the design and conceptualization of the database. OSM and HS led data collection. OSM performed the analyses. All authors contributed equally to writing and editing the manuscript.

Chapter 5 is written in the style of an article appropriate for *Conservation Letters* as: Middleton, O. S., J. P. W. Scharlemann, E. J. Lundgren, C. J. Sandom. “Evidence-based trophic rewilding is geographically limited by contextually biased knowledge of species interactions”. *Conservation Letters*.

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The author contributions are: OSM, EJM, and EW contributed to the conception of the manuscript. OSM led data collection, analyses, results interpretation, and wrote the first manuscript draft. OSM, EJM, ADW, JPWS, and CJS contributed equally to developing the manuscript. All authors contributed equally to revising the final manuscript.

I, Owen Middleton, hereby declare that this thesis has not been, and will not be, submitted in whole or in part to another university for the award of any other degree.

Brighton,
22nd September 2021

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Doctoral thesis submitted for the award of PhD in Biology

**Learning from the past to restore trophic complexity with carnivorous
mammals in the Anthropocene**

by Owen Middleton

Abstract

The structure of the world's mammal communities had remained remarkably consistent for millions of years before modern humans (*Homo sapiens*) encountered them. However, following their global dispersal during the Late Pleistocene (~130,000 – 11,700 years ago), humans began modifying the structure of mammal communities by driving global and local extinctions. Human-induced extinctions were biased towards the largest mammals, which reduced ecosystem trophic complexity by removing top-down interactions that influence ecological dynamics. By acknowledging these past impacts, conservationists now recognise the potential benefits to reversing them through restoring species that are missing from ecosystems. In this thesis, I investigated the extent of modification to terrestrial carnivorous mammal communities as well as the existing opportunities to restore trophic complexity through (i) recolonisations, (ii) reintroductions, and (iii) former introductions. I show that defaunation disproportionately affected once widespread and diverse large-bodied hypercarnivorous mammals, with those remaining being smaller-bodied and less carnivorous. Yet, if extant hypercarnivores recolonised their past geographic ranges, I found that structural modifications to hypercarnivore assemblages could largely be reversed across Africa, much of Eurasia and, to an extent, North America. As a complement to recolonisations, I show that geographically widespread opportunities for evidence-based reintroductions exist, but future research of species interactions should prioritise unstudied environmental contexts

to increase opportunities further. Finally, for mainland Australia, the continent most affected by past human-induced extinctions, I found that formerly introduced carnivorous mammals could act as counter-currents to past defaunation, particularly in contexts without the widespread persecution of an apex predator. Overall, the findings in this thesis reveal diverse opportunities to restore ecosystem trophic complexity with carnivorous mammals across the world to reverse past, and ongoing, human impacts in the Anthropocene.

“A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise.”

Aldo Leopold

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Looking back at this work, it's hard to believe it took four years to complete. I guess it's because a PhD is like a rocky road. Not, the sweet, marshmallow-filled snack. More like an old, poorly-surfaced road with lots of potholes that could throw you off course at any moment – like a global pandemic – but will ultimately get you to your destination if you persist. I owe thanks to many wonderful people and animals for keeping me on course and getting me to this destination.

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CHAPTER 1 | General introduction

“Cherish the natural world, because you’re a part of it and you depend on it.”

Sir David Attenborough

1.1 | Introduction

Across the world, humans (*Homo sapiens*) have altered the functioning of ecosystems upon which all life depends (Vitousek *et al.*, 1997). Ecosystem functioning is, in part, determined by the structure of ecological communities, including the traits of species present and the interactions that emerge between those species (Chapin *et al.*, 1997). Those ecological interactions in turn drive key ecological processes (e.g. predation and herbivory) that influence ecosystem processes (e.g. nutrient dispersal) which contribute to the functioning of ecosystems (Reiss *et al.*, 2009; Akçakaya *et al.*, 2020). The structure of the world’s mammal communities had remained remarkably consistent for millions of years until humans dispersed out of continental Africa during the Late Pleistocene (Stegner & Holmes, 2013; Svenning, Munk & Schweiger, 2019; Blanco *et al.*, 2021). Since then, humans have modified, and continue to modify, the structure of mammal communities through defaunation - i.e. declines of both species and abundance (Dirzo *et al.*, 2014) – which disproportionately affected large-bodied consumers (Smith *et al.*, 2018a; Pacifici *et al.*, 2020), as well as the introduction of species (Wardle *et al.*, 2011). The removal of top-down interactions (henceforth, “trophic downgrading”) from large-bodied consumers can have cascading effects on ecosystem functioning (Estes *et al.*, 2011), while interactions from introduced species are typically linked to environmental degradation or further extinctions (Salo *et al.*, 2007). Overall, the severity of modifications to ecological communities as a whole, alongside increasing rates of land-use change, consumption, and trade, causes many to argue Earth has entered a new geological epoch in which species extinctions will continue without societal change, the Anthropocene (Malhi, 2017; Davis, Faurby & Svenning, 2018; Cooke, Eigenbrod & Bates, 2019).

To halt our impacts on the natural world, conservation has largely focused on protecting habitats and native species compositions, while an increased appreciation for protecting ecosystem functioning has recently occurred (Mace, 2014). Unfortunately, these efforts have been largely ineffective at halting global biodiversity loss (Tittensor *et al.*, 2014). In the Anthropocene, the widespread emergence of novel ecosystems - i.e. ecosystems with new abiotic or biotic factors created by human actions - and impending global change ensures conservation efforts focused solely on preserving native habitats or species compositions from arbitrary historical baselines will become increasingly unrealistic (Hobbs, Higgs & Harris, 2009). Instead, maximizing the capacity for ecosystems to adapt to environmental disturbances will become more necessary and require assessments of ecological community structures using ‘taxon-free’ metrics that involve species’ functional traits and ecological interaction networks (Barnosky *et al.*, 2017). For example, understanding structures of ecological interaction networks has been suggested as a way to focus conservation efforts, as opposed to solely the identity of species within networks (Tylianakis *et al.*, 2010). Studies of ecological community structures through a functional lens have increased exponentially and, despite a wide range of methods existing (e.g. functional dendrograms or multi-dimensional trait spaces), conceptual frameworks are increasingly available to guide hypothesis testing in conservation (Boersma, Kate *et al.*, 2016; Mammola *et al.*, 2021). Using such frameworks, lessons can be learnt from the structure of ecological communities before human impacts began to provide necessary ecological and evolutionary context to guide conservation efforts in the Anthropocene (Barnosky *et al.*, 2017; Leclère *et al.*, 2020).

Rewilding is an emerging conservation strategy that aims to restore ecosystem dynamics, including trophic complexity and dispersal capabilities, instead of particular biodiversity compositional states (Perino *et al.*, 2019). In this sense, rewilding requires contextualizing the present ecological state of an ecosystem, or landscape, by acknowledging ecosystem dynamics before human impacts began, including vegetation communities and missing species. While the meaning of the term ‘rewilding’ has fluctuated since its original conception (Soulé & Noss, 1998), it is typically recognized today as a spectrum from ‘passive rewilding’, which aims to increase habitat connectivity by limiting human management of landscapes, to ‘trophic rewilding’ (Perino *et al.*, 2019; Noss, 2020). Trophic rewilding aims to restore ecological community structures, and reverse trophic downgrading, by reintroducing, or introducing ecologically similar,

populations of apex consumers to restore top-down ecological interactions (Svenning *et al.*, 2016; Galetti *et al.*, 2017) while following guidelines proposed by the IUCN (International Union for Conservation of Nature) (IUCN/SSC, 2013). Trophic rewilding has its critics (e.g. Rubenstein & Rubenstein, 2016), but its advocates argue trophic rewilding could establish self-regulating and biodiverse ecosystems.

Facilitating the widespread restoration of ecosystem trophic complexity in conservation has its challenges. These include but are not limited to: (i) recognizing the extent, and potential ecological consequences, of past trophic downgrading; (ii) concerns surrounding unanticipated ecological outcomes from the return of previously missing species, and (iii) intensive management of novel ecosystems because of perceived ecological harm. These challenges are being increasingly met by a growing body of research that utilizes trait-based approaches to contextualize the effects of past human-induced defaunation and management of novel ecosystems. Such approaches provide additional ecological and evolutionary evidence for conservation decisions to restore and maintain functioning ecosystems in the Anthropocene. In this thesis, I addressed these challenges for carnivorous mammals, a functional group that has experienced widespread declines and remain threatened across the world's ecosystems (Ripple *et al.*, 2014), by using trait-based approaches to investigate the extent to which trophic complexity could be restored in the Anthropocene.

1.2 | Trophic downgrading throughout the late Quaternary

Humanity's impact across the world's ecosystems has resulted in widespread defaunation (Dirzo *et al.*, 2014). In the past 50 years alone, monitored vertebrate populations have declined by an average of 68% (Almond, Grooten & Petersen, 2020) and 20% of 204 mammal species, that broadly represent biomes and taxonomic groups, lost >50% of their geographic range (Pacifi *et al.*, 2020). The primary drivers of such biodiversity loss are attributed to land-use change (Newbold *et al.*, 2015), over-hunting (Benítez-López *et al.*, 2017), and invasive species (Doherty *et al.*, 2016), all of which are driven, or exacerbated, by humans. These drivers disproportionately influence large vertebrate populations (Benitez-Lopez *et al.*, 2019; Newbold *et al.*, 2020). The ecological consequences of large vertebrate population declines include the widespread loss of top-down interactions that disproportionately influence the fertility and functioning of entire ecosystems (Estes *et*

al., 2011; Dirzo *et al.*, 2014; Enquist *et al.*, 2020). Without humanity changing its relationship with the natural world, the decline of the largest remaining species is predicted to continue in the Anthropocene (Davis *et al.*, 2018; Cooke *et al.*, 2019).

The fossil record reveals that human-driven trophic downgrading actually began much earlier, during the Late Pleistocene (Sandom *et al.*, 2014b; Andermann *et al.*, 2020). The cause of the Late Pleistocene extinctions remains contested, with an ongoing debate over whether overhunting by humans or changing climates was the primary driver (Martin, 1963; Barnosky, 2004; Brook & Johnson, 2006; Koch & Barnosky, 2006; Ripple & Van Valkenburgh, 2010; Wroe *et al.*, 2013; Johnson *et al.*, 2016; Saltr  *et al.*, 2016; Van Der Kaars *et al.*, 2017). However, extinctions are rarely caused by a single driver (Wroe *et al.*, 2004) and the interacting effects of climate change and human impacts have been suggested to have driven megafauna extinctions (Broughton & Weitzel, 2018; Saltr  *et al.*, 2019). Regardless of the primary driver, the down-sizing of the world's mammal communities relative to those that occurred for millions of years in the past is predicted to have widespread consequences for the functioning of ecosystems today (Malhi *et al.*, 2016; Enquist *et al.*, 2020). By the end of the Late Pleistocene, approximately two-thirds of the world's megafauna were extinct (Turvey & Crees, 2019). In turn, megafaunal prey decline contributed to the extinction of a once widespread guild of megacarnivores (>100 kg) (Sandom *et al.*, 2018b). Collectively, key ecosystem processes such as nutrient dispersal severely declined following the loss of large home ranges and consumption rates of megafauna (Doughty *et al.*, 2016; Galetti *et al.*, 2018; Berti & Svenning, 2020). While individual interactions were lost, entire interaction networks were also affected by human-driven extinctions, as demonstrated by the instability of predator-prey trophic interaction networks in the Americas following human-induced extinctions (Guimar es *et al.*, 2015; Pires *et al.*, 2020) as well as in ancient Egypt (Yeakel *et al.*, 2014).

1.3 | Restoring trophic complexity through rewilding

There is still time to bend the curve of biodiversity loss if society focused on sustainable development and ambitious conservation strategies (Lecl re *et al.*, 2020). To encourage this societal shift, the United Nations has designated 2021-2030 as the Decade on Ecosystem Restoration to encourage globally widespread efforts to reverse biodiversity loss and environmental degradation (<https://www.decadeonrestoration.org/>). During this

decade, maximizing habitat connectivity to facilitate recolonisations, as well as the reintroduction of missing apex consumers, is argued to be required if we are to re-establish ecologically complex and resilient ecosystems (Perino *et al.*, 2019; Svenning, 2020).

Rewilding efforts aim to restore trophic complexity by reinstating species and their ecological interactions (Fernández, Navarro & Pereira, 2017). The ecological processes restored by returning species would largely be determined by two key functional traits of the species involved: body mass and diet (Price & Hopkins, 2015). A species' body mass largely determines its role within an ecological interaction network, for example the size, or amount, of resource(s) consumed (Wheelwright, 1985; Carbone *et al.*, 1999). A species diet will, in turn, determine the type of interaction network it participates, for example mutualistic (e.g. frugivores in seed dispersal networks) or antagonistic networks (e.g. predators in predator-prey networks) (Tylianakis *et al.*, 2010). Many species also interact within more than one network type (Pires, 2017). Mammals, for example, can have diverse diets (Pineda-Munoz & Alroy, 2014), with omnivorous species consuming both live prey and fruits and thus contributing to multiple interaction networks (Rosalino, Rosa & Santos-Reis, 2010). Even hypercarnivores ($\geq 70\%$ vertebrate biomass in diet (Van Valkenburgh, 1991)) can contribute to secondary seed dispersal through the consumption of frugivorous prey species – a process known as diploendozoochory (Hämäläinen *et al.*, 2017).

Regardless of the interaction networks involved, rewilding aims to increase the diversity of ecological interactions to restore, or reinforce, ecological processes and ecosystem functioning (Svenning *et al.*, 2016) – often referred to as interaction network 'rewiring' (Pires, 2017). Increasing the number of interactions, and the number of species contributing to the same ecological processes, would increase the resilience of entire ecosystems to impending global change (Perino *et al.*, 2019). In a warming Arctic, top-down interactions from herbivores can regulate expansion and growth of shrubs that would otherwise cause a regime shift towards alternate shrub-dominated states with far-reaching consequences (Kaarlejärvi, Hoset & Olofsson, 2015; Vowles & Björk, 2019). Further, apex predator persecution in Australia can shift ecosystems to bottom-up driven states with high mesopredator populations which, particularly for introduced species, are typically perceived to be ecologically harmful (Wallach *et al.*, 2010). In these ecosystems, respectively, maintaining populations of large-bodied herbivores and an apex predator,

and hence maintaining trophic complexity, would promote resilience to shifts towards alternative ecological states.

Unintentional and intentional rewilding projects have facilitated the recovery of locally extirpated species across the world. Passive rewilding has occurred across much of Europe through rural land abandonment which, in combination with species having more legal protection than ~50 years ago, has resulted in carnivores recolonising their former geographic ranges across much of mainland Europe (Chapron *et al.*, 2014). Active reintroductions (i.e. trophic rewilding) successfully reinstated missing ecological interactions that influence community dynamics following the reintroduction of grey wolves (*Canis lupus*) to the Yellowstone National Park (Ripple & Beschta, 2012a) and of two frugivores, red-rumped agouti (*Dasyprocta leporina*) and howler monkeys (*Alouatta guariba*) in the Atlantic Forests of Brazil (Fernandez *et al.*, 2017; Genes *et al.*, 2017, 2019). The overall size and resilience of entire seed-dispersal networks was also found to increase following large herbivore reintroductions to the Gorongosa National Park in Mozambique (Correia *et al.*, 2017).

Restoring top-down interactions through facilitating recolonisations or species reintroductions may not be an option across much of the world as many species have become globally extinct (Schowanek *et al.*, 2021). Introducing species for conservation purposes that are functionally similar as ecological replacements may instead be required and the IUCN has guidelines for when they are perceived as appropriate (IUCN/SSC, 2013). Examples of ecological replacements successfully restoring top-down interactions is largely restricted to herbivory on islands to date (Seddon *et al.*, 2014). For example, Aldebran giant tortoises (*Aldabrachelys gigantea*) and radiated tortoises (*Astrochelys radiata*) introduced to Mauritius successfully restored grazing regimes which benefited native plant populations (Griffiths *et al.*, 2011).

Species that were introduced for non-conservation purposes are typically regarded as undesirable or ecologically harmful that require control (Eldridge, Ding & Travers, 2020; Castelblanco-Martínez *et al.*, 2021). However, many herbivorous megafauna have been widely introduced into areas that once harbored a diverse guild of ecologically comparable species that are now-extinct, leading many to argue that they provide an unintentional trophic rewilding opportunity (Dembitzer, 2017; Lundgren *et al.*, 2018; Monsarrat, Hansen & Svenning, 2020). A meta-analysis even found that trophic cascades

induced by these species are typically comparable to intentionally reintroduced species (Tanentzap & Smith, 2018). The extent to which species that have been introduced to areas outside of their geographic ranges could restore trophic complexity, but are not large-bodied mammalian herbivores, remains unknown.

1.4 | Carnivorous mammals

Since the extinction of the dinosaurs, and the onset of the Cenozoic Era (~66 mya, million years ago), mammalian carnivores have largely dominated the top of the food chain in terrestrial ecosystems. The evolutionary origin of mammalian carnivores began during the early Cenozoic with the rise of the sister-taxa carnivoramorpha and creodonts (Wesley-Hunt & Flynn, 2005), alongside the mesonychids which likely evolved into cetaceans (Van Valkenburgh, 1999). Throughout the Cenozoic, convergent evolution of predator traits occurred with the evolution of bone-crackers, omnivores, and saber-toothed species across continents (Van Valkenburgh, 1999). However, the taxon representing the largest hypercarnivores in ecosystems has fluctuated throughout the history of mammalian evolution (Valkenburgh *et al.*, 2014). Such fluctuations is thought to be caused by the vulnerability of hypercarnivores to environmental disturbances because of their extreme reliance on large prey (Van Valkenburgh, 1999).

Mammalian carnivores are often regarded as species from the eutherian Order *Carnivora* (e.g. Dalerum 2013). However, as a feeding guild, mammalian carnivores include any mammal which consumes animal matter, and so include species such as carnivorous marsupials (Jones, 2003). Species are typically referred to as carnivores if at least half of their diets are of animal biomass (Van Valkenburgh, 1999). Species with more specialized carnivorous diets are often referred to as ‘hypercarnivores’, which consume $\geq 70\%$ vertebrate meat (Van Valkenburgh, 2007). In addition, most carnivores vary in the degree to which they scavenge for meat, with implications for their ecological roles in a given ecosystem (Kane *et al.*, 2017; O’Bryan *et al.*, 2018).

The ecological processes of predation and scavenging have different ecosystem-level effects. Predators actively kill or subdue live animal prey for consumption and their presence therefore creates a risk of predation for prey animals (Brown, Laundré & Gurung, 1999). Risk of predation can be variable in a heterogenous environment, which can therefore create a ‘landscape of fear’ in which the fear of predation for prey animals

is perceived to vary (Laundre, Hernandez & Ripple, 2010). Landscapes of fear can influence the distribution of large herbivore prey which influences their foraging behavior and the associated pressures on vegetation structures (Ripple & Beschta, 2004). Active predators also have the capacity to numerically regulate prey population sizes (Salo *et al.*, 2010). Alternatively, scavenging is the consumption of dead animal matter that is not actively predated. Scavengers can be either obligatory, and depend upon carrion, or facultative whereby they opportunistically consume carrion (Wilson & Wolkovich, 2011).

1.5 | Reasons for restoring trophic complexity with carnivorous mammals

Despite the roles that carnivorous mammals have played in ecosystems for millions of years, they are now widely threatened by human impacts (Ripple *et al.*, 2014). Compared to their historic geographic ranges, 17 of 43 North American carnivorous mammal species have recently lost >20% their range (Laliberte & Ripple, 2004) with many of the world's larger-bodied carnivorous mammals being reduced to <10% of their historic ranges (Wolf & Ripple, 2017). Yet, if prehistoric geographic ranges were considered, the extent of carnivorous mammal range loss would likely be even greater (Svenning *et al.*, 2016). Such declines likely resulted from prey loss which remains a key threat today (Wolf & Ripple, 2016; Sandom *et al.*, 2018b), alongside other environmental disturbances such as land-use change (Newbold *et al.*, 2020).

Apex predators can influence the behavior and population dynamics of their prey (Salo *et al.*, 2010; Glen & Dickman, 2014; Letnic & Ripple, 2017) and mesopredators (Ritchie & Johnson, 2009). Therefore, the decline, or entire removal, of apex predators in ecosystems around the world is predicted to cause widespread trophic cascades resulting in vegetation biomass declines and mesopredator population increases (Hoeks *et al.*, 2020). In response, mesopredator populations are typically subject to lethal control by humans (Wallach, Ripple & Carroll, 2015b). However, maintaining predator assemblage structures and top-down pressures from protected apex predators on mesopredators would likely act as an ecosystem service irreplaceable by human management (Prugh & Sivy, 2020). As such, there are increasing calls to restore missing carnivore populations and

their ecological effects in ecosystems (Hunter *et al.*, 2015; Newsome *et al.*, 2015; Sanderson *et al.*, 2021).

The recycling of carrion is another critical ecosystem service provided by carnivores. As is the case for active predation, consuming decaying animal biomass limits the transmission of zoonotic diseases (O'Bryan *et al.*, 2018). In India, declining vulture (*Gyps spp.*) populations have been linked to increasing wild dog (*Canis familiaris*) populations because of a reduction in competition for food sources (Markandya *et al.*, 2008). This could lead to an increase in dog bites and rabies transmissions to humans (O'Bryan *et al.*, 2018). Scavengers also provide regulatory service to humans, with golden jackals (*Canis aureus*) across Europe estimated to save >\$0.5 million in waste control that could have contaminated groundwater (Ćirović, Penezić & Krofel, 2016). In the UK, 76% roadkill animals are removed within 12 hours which are consumed by the scavenger community, including corvids (Family: *Corvidae*), common buzzards (*Buteo buteo*), and red foxes (*Vulpes vulpes*) (Schwartz *et al.*, 2018). Scavengers also facilitate the stabilization of food webs by forming low-intermediate interactions with multiple prey species (McCann, Hastings & Huxel, 1998).

These widely missing ecological effects across many of the world's ecosystems could be restored through facilitating natural recolonizations (Elmhagen *et al.*, 2010) or active reintroductions of carnivorous mammals (Ripple & Beschta, 2004; Jiménez *et al.*, 2019). Such efforts would rewire interaction network structures that were otherwise simplified by extinctions and increase ecosystem resilience (Svenning *et al.*, 2016; Wolf & Ripple, 2018). Such rewiring could restore structure to ecological communities by regulating the effects of herbivores as well as mesopredators, the latter of which have their ecological effects mediated by the web of intra-guild interactions that occur within the predator community (Palomares & Caro, 1999), depending upon predator diversity (Finke & Denno, 2004) and prey-size ratios between predators (Donadio & Buskirk, 2006; Krensek & Rudolf, 2014).

1.6 | Challenges to restoring trophic complexity with carnivorous mammals

Across much of the world, wild carnivorous mammal populations, including apex predators, are managed to some degree, although the extent of which depends upon the species of carnivore and local social, economic, and ecological context (Treves & Karanth, 2003; Bruskotter *et al.*, 2017; Lozano *et al.*, 2019). Widespread human conflict drives such management decisions which is typically in response to livestock predation (Sillero-Subiri & Laurenson, 2001; Woodroffe & Frank, 2005) or removing perceived threats of livestock predation (Levy, 2009), although both are exacerbated by habitat and prey loss following the expansion of agriculture or resource extraction projects (Baker *et al.*, 2008). However, carnivore management can actually increase livestock predation by disturbing social dynamics (Allen & Gonzalez, 1998; Allen, 2014; Treves, Kropfel & McManus, 2016). Farmers often associate the term ‘rewilding’ solely with carnivore reintroductions, creating polarized views of trophic rewilding among critical stakeholders because of perceived threats to livestock (Sandom *et al.*, 2018a). Even carnivores that are naturally recolonising areas of their former geographic range face negative attitudes from rural resident and farmers who, in North America, tend to be against their protected status (Smith, Nielsen & Hellgren, 2014). In contrast, European rural land abandonment through rural to urban migration is increasing available habitat for carnivores to recolonise (Chapron *et al.*, 2014). Further, predator-friendly farming methods are increasingly used, including livestock guardian dogs or use of technology, which can be successful at protecting both livestock and wild carnivores (Johnson & Wallach, 2016). As such, recolonisation potential for carnivorous mammals may increase in the future.

Concerns are often raised about whether reintroducing carnivorous mammals, and any species in general, will have the desired ecological outcome (e.g. Nogués-Bravo *et al.*, 2016). These concerns are justified because of the context-dependencies of predator-prey interaction outcomes (Early & Keith, 2019) or the amount of predation or scavenging performed by carnivores (Pereira, Owen-Smith & Moleón, 2014). For example, various abiotic and biotic conditions have been shown to influence the direct interactions that collectively form species diets (Dorresteijn *et al.*, 2015; Haswell, Kusak & Hayward, 2017). Further, trophic cascades following carnivore reintroductions can also vary in magnitude depending on the local environmental context (Eisenberg, Seager & Hibbs,

2013). To overcome such limitations, practitioners and conservationists could recognize limits to current knowledge and identify future research prioritizations by acknowledging the environmental contexts in which we already understand the ecological effects of a given species (Bezanson & McNamara, 2019; Britnell *et al.*, 2021). The collection and analysis of context-specific quantitative data could then be used to forecast reintroduction outcomes as a form of risk-assessment (Baker, Gordon & Bode, 2017; Pires, 2017).

Introduced predators in novel ecosystems are typically linked to the decline of biodiversity (Loss, Will & Marra, 2013). However, there is typically little acknowledgement of these undesired effects as being context-dependent (Rayner *et al.*, 2007; Wallach *et al.*, 2015b). For example, while introduced mesopredators in Australia (e.g. red foxes and cats) are widely persecuted because they are linked to native species population declines (Woinarski, Burbidge & Harrison, 2015; Woinarski *et al.*, 2017; Doherty *et al.*, 2017b), their populations and behavior have widely been shown to be influenced by dingoes, Australia's apex predator. Yet, dingoes are often labelled as 'wild dogs' and pests by the livestock industry, resulting in their widespread persecution (Levy, 2009) that influences their social stability and capacity to place top-down pressures on mesopredators (Wallach *et al.*, 2009).

Learning from past defaunation and past ecological communities, alongside existing knowledge of species ecological functions, could contribute to overcoming challenges to restoring trophic complexity with carnivorous mammals in the Anthropocene. Using trait-based approaches would facilitate the possibility to exploring what ecological functions could be restored in the Anthropocene through: (i) recolonisations, (ii) reintroductions, and (iii) former introductions. Addressing these knowledge gaps would have implications for conservation policy and future research prioritization given the urgency required to restore functioning ecosystems in the UN's Decade on Ecosystem Restoration to prepare for future global change.

1.7 | PhD aim and structure

The aim of this thesis was to investigate the extent to which ecosystem trophic complexity could be restored with carnivorous mammals through multiple strategies along a gradient from passive with native species to active (at least, actively introduced in the past) with non-native species. These include (i) recolonisations under a scenario of maximized

dispersal capacities, (ii) evidence-based reintroductions, and (iii) former introductions when contextualized by past defaunation (Fig. 1.2). To do this, I utilized ‘taxon-free’ methods from community ecology, involving functional traits and interaction data, alongside palaeoecological insights of species’ past geographic distributions. The five main analytical chapters of this thesis (Chapter 2-6) cover topics from human-induced defaunation to identifying existing limits and opportunities in the geographic scope for trophic rewilding to restore trophic complexity in the Anthropocene. Each chapter was written as an independent article that has either been published, submitted, or is suitable for submission for peer-review in a scientific journal.

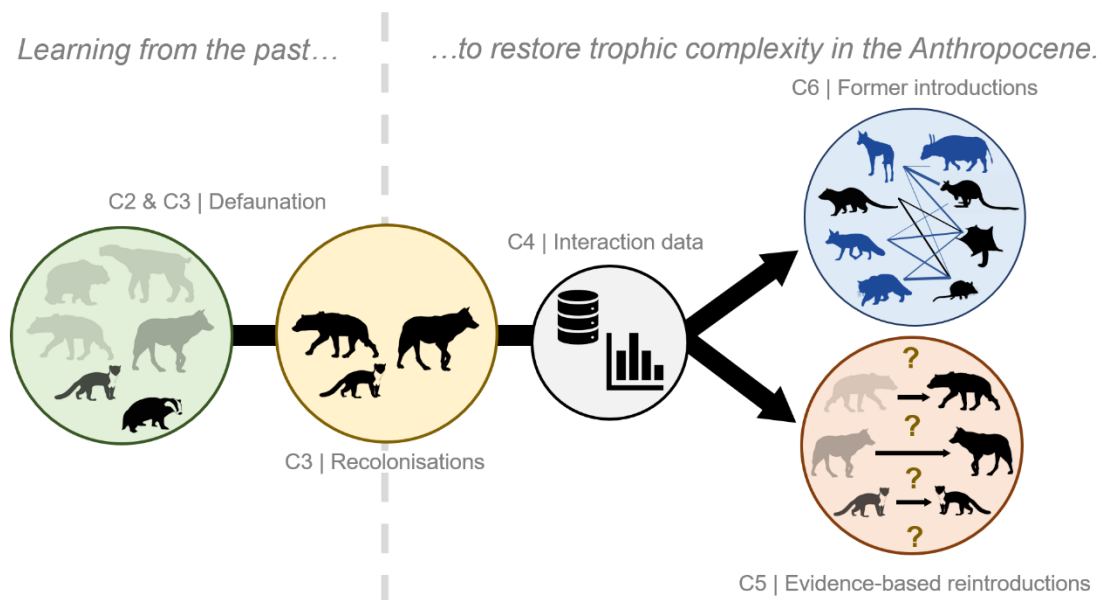


FIGURE 1.2 | Schematic diagram describing the flow of the thesis and core content of the analytical chapters (Chapter 2 to 6). Each chapter explored a self-contained but complimentary piece of work to the overall thesis. These involved learning from the past (*Chapter 2 and Chapter 3*) to explore opportunities to restore trophic complexity in the Anthropocene through recolonisations (*Chapter 3*) and, in combination with novel interaction data (*Chapter 4*), evidence-based reintroductions (*Chapter 5*) and formerly introduced species (*Chapter 6*).

In *Chapter 2*, I investigated the extent of prehistoric and historic human-induced defaunation to carnivorous mammal ensembles across the world’s continents throughout the late Quaternary (~130,000 ybp – present day). Using two functional traits at the species-level that broadly captures a species’ contribution to the ecological processes of predation and scavenging, body mass and diet composition (i.e. average consumption of vertebrate, invertebrate, and plant biomass [%]), I assessed whether defaunation was

selective towards species with certain functional trait compositions. The major contribution of this chapter is by including all mammal species that share ecological processes, rather than merely their taxonomic identity, and therefore investigating trophic downgrading at a wider geographic scope than previous research.

In *Chapter 3*, I used functional traits describing the ecological effects of hypercarnivorous mammals as predators to identify how hypercarnivore assemblages were modified by extinctions and geographic range contractions. I then investigated how recolonisations of extant hypercarnivores could restore assemblage structures across the world. The major contribution of this chapter is it being the first global assessment of how natural recolonisations alone could reverse past human-induced defaunation.

The diet traits used in *Chapters 2 and 3*, as in mammalian functional ecology in general, are typically global, species-level averages which prohibits any consideration of intra-specific population-level trait variability that is relevant for conservation and trophic rewilding in practice. To address this limitation I developed, and in *Chapter 4* describe, an open-access database (CarniDIET) that contains georeferenced quantitative diet data for 103 of the world's carnivorous mammals that were collated from the primary literature. CarniDIET describes population-level trophic interactions between carnivores and their resources that could generate region-specific trait values, or to look at variability in the characteristics of prey species consumed across environmental gradients. While a qualitative interaction database already existed, the major advancement of CarniDIET is attributing, at the population level, interaction strengths to their resources.

In *Chapter 5*, I used CarniDIET to identify the geographic scope for trophic complexity restoration through evidence-based reintroductions for 43 extirpated carnivorous mammals. While geographic biases in ecological research are well known, the potential biases that may arise in our understanding of species' ecologies through geographic bias in species-specific research has only relatively recently been discussed. The major contribution of this chapter is being the first attempt to quantify how representative current knowledge of species' ecological interactions are across the range of environments in which they occur. As a common concern with trophic rewilding revolves around unanticipated ecological outcomes of reintroductions, such an assessment is useful to understand where evidence-based trophic rewilding could occur and areas where future research would still be required to facilitate this.

In *Chapter 6*, I used CarniDIET to investigate whether recently established mammal species, that were introduced by humans for non-conservation purposes and are now heavily persecuted, have the capacity to restore trophic complexity in Australian ecosystems. I contextualize their impacts through comparing extinct and extant predator functional trait compositions and whether the emergent structure of otherwise simplified ecological interaction networks have been rewired to resemble those before human-driven extinctions. The major contribution of this chapter is the re-examination of an ongoing conservation issue by using taxon-free metrics and comparing the potential impacts of recently established predators to those that went extinct in prehistory alongside the effects of widespread wildlife management of apex predator persecution.

A general discussion is presented in *Chapter 7*, which synthesizes the results of each chapter in relation to one another, their potential influence on conservation policy, and future research suggestions.

CHAPTER 2 | Homogenization of carnivorous mammal ensembles caused by global range reductions of large-bodied hypercarnivores during the late Quaternary

*“We live in a zoologically impoverished world, from which all the hugest and fiercest,
and strangest forms have recently disappeared...”*

Alfred Russell Wallace.

2.1 | Abstract

Carnivorous mammals play crucial roles in ecosystems by influencing prey densities and behaviour, and recycling carrion. Yet, the influence of carnivores on global ecosystems has been affected by extinctions and range contractions throughout the Late Pleistocene and Holocene (~130 000 years ago to the current day). Large-bodied mammals were particularly affected, but how dietary strategies influenced species' susceptibility to geographic range reductions remains unknown. We investigated 1) the importance of dietary strategies in explaining range reductions of carnivorous mammals ($\geq 5\%$ vertebrate meat consumption), and 2) differences in functional diversity of continental carnivore ensembles by comparing current, known ranges to current, expected ranges under a present-natural counterfactual scenario. The present-natural counterfactual estimates current mammal ranges had modern humans not expanded out of Africa during the Late Pleistocene and were not a main driver of extinctions and range contractions, alongside changing climates. Ranges of large-bodied hypercarnivorous mammals are currently smaller than expected, compared to smaller-bodied carnivorous mammals that consume less vertebrate meat. This resulted in consistent differences in continental functional diversity, whereby current ensembles of carnivorous mammals have undergone homogenisation through structural shifts towards smaller-bodied insectivorous and herbivorous species. The magnitude of ensemble structural shift varied

among continents, with Australia experiencing the greatest difference. Weighting functional diversity by species' geographic range sizes caused a three-fold greater shift in ensemble centroids than when using presence-absence alone. Conservation efforts should acknowledge current reductions in the potential geographic ranges of large-bodied hypercarnivores and aim to restore functional roles in carnivore ensembles, where possible, across continents.

2.2 | Introduction

In the coming century, anthropogenic extinctions are predicted to shift global mammal assemblages towards small-bodied insectivores (Cooke *et al.*, 2019). Yet, mammal extinctions influenced by humans are not only a future, or recent, phenomenon but began during the Late Pleistocene (130 000 to 11 700 years ago) and continued throughout the Holocene (11 700 years ago to the current) (Burney & Flannery, 2005; Turvey & Fritz, 2011; Smith *et al.*, 2018a), henceforth collectively referred to as the late Quaternary. During the Late Pleistocene, modern humans expanded out of Africa in waves (Timmermann & Friedrich, 2016) and colonised the inhabited continents, which, in combination with changing climates (Barnosky, 2004; Pushkina & Raia, 2008; Cooper *et al.*, 2015), caused globally widespread mammal range modifications and extinctions (Stuart *et al.*, 2004; Sandom *et al.*, 2014a; Johnson *et al.*, 2016; Araujo *et al.*, 2017). Mammal assemblages were further modified by direct human-induced range contractions of extant species during the Holocene (Wilson *et al.*, 2016; Wolf & Ripple, 2017). Large-bodied mammals on continents were particularly susceptible to range reductions (extinctions and range declines, collectively) throughout the late Quaternary (Smith *et al.*, 2018a), which reduced ecological processes such as nutrient and seed dispersal (Doughty *et al.*, 2016; Galetti *et al.*, 2018). However, knowledge is limited on whether certain dietary strategies influenced species' susceptibility to late Quaternary range reductions. Here, we address this knowledge gap for carnivorous mammals by investigating whether late Quaternary range reductions were biased towards hypercarnivorous species (those consuming $\geq 70\%$ vertebrate meat (Valkenburgh, 1988; Holliday & Stepan, 2004)), and how continental ensembles of carnivorous mammals were modified since modern humans expanded out of Africa. We refer to continental ensembles as pools of species in specified

geographic areas (i.e. continents) consuming a shared resource (vertebrate biomass) and are phylogenetically restricted (Mammalia) (Fauth *et al.*, 1996).

Diet is a crucial ecological trait, which interacts with body mass to influence behaviour (Price & Hopkins, 2015) and ecological function (Duffy, 2002). Mammals with carnivorous diets consume animal biomass following hunting or scavenging (Wilson & Wolkovich, 2011). Ecological effects of predatory carnivores include the potential to influence the behaviour and populations of their prey (Ripple & Beschta, 2012a). Indirectly, these interactions can influence vegetation consumption rates and patterns (Atkins *et al.*, 2019), and prevent mesopredator release (Prugh *et al.*, 2009). Scavengers contribute to nutrient cycling by consuming carrion, which can stabilise food webs (Wilson & Wolkovich, 2011). However, carnivore extinctions (Dalerum *et al.*, 2009) and widespread range contractions of extant carnivores (Laliberte & Ripple, 2004; Wolf & Ripple, 2017) have occurred in response to anthropogenic pressures, including habitat fragmentation (Di Minin *et al.*, 2016; Newbold *et al.*, 2020), prey depletion (Wolf & Ripple, 2016; Sandom *et al.*, 2018b), and direct persecution (van Eeden *et al.*, 2017). Such recent effects of modern humans on carnivorous mammals may mirror prehistorical ones, particularly, the reduction of prey diversity and abundance (Sandom *et al.*, 2018b).

Diets are typically variable, and it is uncommon for species to be true dietary specialists with only 23.7% of mammals primarily consuming a single food type (e.g. vertebrate meat or fruit) (Pineda-Munoz & Alroy, 2014). However, hypercarnivores, like Felidae, are true specialists of vertebrate meat (Valkenburgh, 1988; Holliday & Stepan, 2004). Throughout mammalian evolution large-bodied, hypercarnivorous clades have evolved and subsequently disappeared, likely unable to adapt to ecological disturbances because of intrinsic traits including specialised resource requirements and slow life-histories (Van Valkenburgh, 1991, 1999). Dietary and behavioural specialism determine a species' ecological niche and influence its ability to respond to disturbances and fluctuation in resource availability (Cardillo *et al.*, 2004; Clavel, Julliard & Devictor, 2011). In stable environments dietary specialists are thought to thrive while preferred resources are abundant, whereas generalists thrive in unpredictable environments with varied resource availability (Griffiths *et al.*, 2011).

Disturbance events can create selection pressures that can be neutral or selective with respect to species' ecological traits (Pakeman, 2011; Mouillot *et al.*, 2013), and can

be represented by changes in the structure of multidimensional functional trait space (Mouillot *et al.*, 2013). Extinctions of large-bodied mammals, in response to modern human arrival (Turvey & Fritz, 2011; Sandom *et al.*, 2014b; Johnson *et al.*, 2016; Araujo *et al.*, 2017) and changing climates (Barnosky, 2004; Pushkina & Raia, 2008; Cooper *et al.*, 2015), was a filtering process that led to functional diversity reduction in North American mammals (Davis, 2017), as well as for Carnivora above 10kg worldwide (Dalerum *et al.*, 2009). In Africa, carnivore functional groups have been largely retained, although previous estimates of continent-wide changes in late Quaternary functional diversity have considered extinctions without considering geographic range contractions of extant species, and so functional diversity declines may be underestimated (Dalerum *et al.*, 2009).

Here, we investigated whether current geographic ranges of hypercarnivorous mammals are more restricted than those of less carnivorous mammals, and consequently how functional diversity of continent-wide ensembles have been affected. We compared the current, known geographic ranges of mammals in response to widespread human presence and changing climates throughout the late Quaternary, to a present-natural counterfactual scenario (Faurby & Svenning, 2015). The present-natural represents current, expected ranges of mammals had modern humans not expanded out of Africa and, alongside changing climates, contributed to late Quaternary range reductions. Comparing current and present-natural ranges provides insights into how prehistoric and historic effects of modern humans, alongside changing climates, influenced the current geographic ranges of carnivorous mammals (Fig. A2.1). We assessed if (i) mammals with more carnivorous diets have larger differences between current and present-natural ranges than mammals with less carnivorous diets, (ii) differences in continental functional diversity of carnivorous mammal ensembles between current and present-natural are consistent and suggestive of trait filtering, and (iii) differences in functional diversity is underestimated when excluding the lost geographic ranges of extinct and extant species.

2.3 | Methods

2.3.1 | Species selection and functional traits

The Phylogenetic Atlas of Mammals database (PHYLACINE v.1.2) was used for species selection (Faurby *et al.*, 2018). Carnivorous mammals were selected as those reported to

consume $\geq 5\%$ vertebrate meat, and to be terrestrial (coded 1 in PHYLACINE) and not aerial, freshwater or marine (0). Humans (Genus: *Homo*) were excluded from our analyses. These criteria returned 1081 species from 15 orders, with 12% classed as hypercarnivorous (Fig. A2.2; those consuming $\geq 70\%$ vertebrate meat (Valkenburgh, 1988; Holliday & Steppan, 2004)).

For each species, we extracted functional traits from Phylacine describing two key dimensions of a species' ecological niche: body mass (g), averaged across sex and geographical location (as previously defined (Smith *et al.*, 2003)), and diet, expressed as the average percentage of food consumed from three resource categories: vertebrate, invertebrate, or plant (for details, see (Faurby *et al.*, 2018)). Although diets vary across time and space (Davis & Pineda Munoz, 2016), the available species-specific diet information is sufficient for macroecological analyses (Faurby *et al.*, 2018).

2.3.2 | Continental ensemble species pools

We used two geographic ranges for mammals from PHYLACINE: current and present-natural (Fig. A2.1), both provided as rasters in Behrmann equal-area projection with raster cell resolution of 9000 km², 1° wide. The current ranges included rasterized native ranges from the IUCN Red List Version 2016-3 (IUCN, 2016). The present-natural ranges, created by Faurby & Svenning (2015), included counterfactual estimates of current, expected ranges for all mammals that have existed during the past 130 000 years, assuming late Quaternary range reductions had not occurred (for methods see Faurby & Svenning (2015)). To create present-natural ranges, all mammals were systematically reviewed for range reductions, except for non-threatened, small-bodied species (< 1kg), assuming these species were not impacted by humans. In total, 51% of species included in our analyses were systematically reviewed. To assess potential bias in our results because of the uneven review of species' range changes, all analyses were performed for all species, and only for species that were systematically reviewed.

Species range rasters were clipped, using 'mask' from the 'raster' package (Hijmans *et al.*, 2019) using R Version 3.5.1 (Team, 2019) to an estimated Late Pleistocene land map (Fig. A2.3) to remove species ranges from islands not connected to continental mainland by land bridges during the last glacial maximum. To measure a species' continental range size, we masked its geographic range raster to a Behrman equal-area projected continental shapefile and summed the number of cells that fell

entirely within a continent's border (ESRI, 2002). For each species, geographic range difference was calculated as the number of raster cells occupied in the current minus the present-natural ranges (Fig. A2.4). Out of 1081 species, 14% had smaller ranges in the current compared to the present-natural. As our focus was on range loss, four species with larger ranges in the current (coyotes, North African white-toothed shrew, least weasel and lesser white-toothed shrew) were classified as having unchanged geographic range.

2.3.3 | Functional diversity of continental ensembles

We calculated functional diversity metrics from functional spaces for each continent and for current and present-natural ranges separately, using the 'FD' package (Laliberté, Legendre & Bill Shipley, 2014). We scaled and centred traits of $\log_{10}$ -transformed body mass and the three dietary traits by subtracting the means and dividing by the standard deviation. To calculate continental functional spaces, we calculated a dissimilarity matrix for all species using Gower's distance because of unequal weighting of traits (body mass: 1, each dietary trait: 1/3). Principal coordinate analysis (PCoA) was performed on the dissimilarity matrix, using the 'dbFD' function which returns PCoA axes to construct functional spaces. We incorporated the first four PCoA axes into our analyses, as recommended by Maire *et al.* (Maire *et al.*, 2015), which captured 73% of trait variation. The variance explained by each axis was calculated by the sum of eigenvector values, divided by the value of each axis. Each PCoA axis was explained by a combination of the original functional traits (Fig. A2.5). A global functional trait space was calculated using all species (Fig. A2.6), with continental functional spaces extracted as subsets of species present in a continental ensemble.

We calculated two functional diversity metrics, functional richness (FRic) (Villéger, Mason & Mouillot, 2008) and functional dispersion (FDis) (Laliberte & Legendre, 2010) for the current and present-natural ensembles for each continent. FRic was calculated as the minimum convex polygon for each continental functional space relative to the global 4-D functional space, scaled from 0 (no functional space) to 1 (global functional space). FRic is unaffected by range size weighting. FDis involves calculating the functional space centroid, which can be weighted by a given metric (i.e. abundance). Here, FDis was calculated first as the average distance of species from the centroid of the species functional space without weighting (i.e. presence/absence) (Fig. A2.5), and second with weighting by each species' continental geographic range, which shifts centroids towards species with larger ranges (Fig. A2.7). Lower values of FDis indicate

higher species similarity, whereas higher values indicate higher species dissimilarity within an ensemble.

2.3.4 | Statistical analyses

2.3.4.1 | Identifying traits influencing differences between current and present-natural geographic ranges

To investigate factors influencing differences between current and present-natural ranges of carnivorous mammals, we fitted binomial Bayesian phylogenetic mixed models (BBPMMs) accounting species' shared ancestry (Harvey & Pagel, 1991) using the 'MCMCglmm' package (Hadfield, 2010a). We used phylogenetic trees from the Phylacine database and took average estimates (log-odds ratios) and upper and lower 95% credible intervals from 100 sampled phylogenetic trees and BBPMM models using the 'mulTree' package (Guillerme & Healy, 2014), to account for phylogenetic uncertainty. The response variable was the proportional range reduction expressed as the number of lost and currently occupied raster cells. We included all species in our models with extinct species ($n = 26$ species) coded as having a 100% range reduction. Scaled and centred predictor variables included body mass ($\log_{10}(g)$) and vertebrate consumption (%).

Each model was run for 200 000 iterations, with burn-in period of 10 000 and thinning interval of 100. We checked model chain convergence using the Gelman-Rubin statistic, the potential scale reduction factor (PSR), with all models having a $PSR < 1.1$ (Gelman & Rubin, 1992). As recommended by Hadfield (Hadfield, 2010b), and as used by Healy et al. (Healy *et al.*, 2014), we used an uninformative inverse-Wishart prior distribution (variance, $V = 0.5$, and belief parameter, $nu = 1$). As in Healy et al. (Healy *et al.*, 2014), we used a hierarchical partitioning method for model selection by running models with each variable individually and with interactions, to identify trait combinations best explaining proportional range reduction. The model structure with the lowest average deviance information criteria (DIC) value was selected as the best-supported model (Healy *et al.*, 2014).

2.3.4.2 | Continental ensemble functional diversity and functional space structural change

To test for differences in FDis and FRic between current and present-natural ensembles, we performed non-parametric Wilcoxon signed-rank tests, using each continent as an independent observation. Differences in continental functional space between current and

present-natural were investigated by assessing magnitude and directional shift of the ensemble centroids. To assess directional difference in functional space, we calculated centroid shifts along each of the four principal coordinate axes from the current to present-natural for each continent. We used Kruskal-Wallis tests to test for differences in the magnitude of centroid shifts between axes for both weighting methods separately. Post-hoc Dunn-tests identified pairwise differences. Mann-Whitney tests were used to investigate differences in magnitude of centroid shifts within each of the four functional space axes when calculating FDis as unweighted (presence-absence) and weighted (geographic range size).

2.4 | Results

2.4.1 | Traits influencing differences between current and present-natural geographic ranges

After controlling for phylogenetic relatedness, the best supported model for predicting species geographic range differences (Table A2.1) included an interaction between body mass and vertebrate consumption (Table A2.2). Increases in body mass resulted in greater geographic range differences (BBPMM; body mass: log-odds ratio estimate [E] = 9.11, credible intervals [CI]: 6.58-11.97), the effect of which increased with higher vertebrate consumption (Fig. 2.1; interaction term: E = 1.52, CI: 0.13-2.97). In re-analyses including only systematically reviewed species, the best supported model was the same (Table A2.3), although the significant interaction between body mass and diet was lost, with body mass being the only significant predictor (Table A2.4; Fig. A2.8).

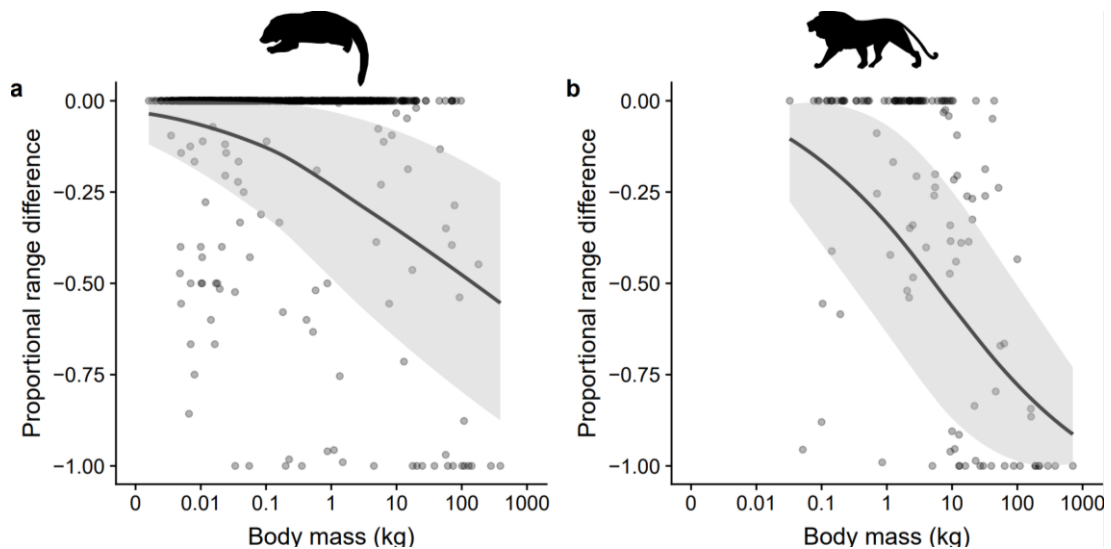


FIGURE 2.1 | Geographic range loss of carnivorous mammals based on average body mass and vertebrate meat consumption. Proportional difference between current and present-natural species' geographic ranges (points with equal transparency) increased with greater body masses ($\log_{10}(\text{kg})$ for interpretability). The effect was greater for species with increased vertebrate meat consumption, shown for illustration for (a) non-hypercarnivores (5-69% vertebrate meat, e.g. binturong), and (b) hypercarnivores ($\geq 70\%$ vertebrate meat, e.g. African lion). Average BBPMM estimate (black line), accounting for shared ancestry, is shown with upper and lower 95% credible intervals (shaded area).

2.4.2 | Continental ensemble structural shifts for carnivorous mammals

All continents experienced similar structural shifts in functional diversity when comparing current to present-natural ensembles when weighted (Fig. 2.2a) by geographic range and unweighted (Fig. A2.9). Current FRic was lower across continents, indicating loss of species with the most extreme traits (median relative decline: -3.9%, lower quartile (Q2): -1.5%, upper quartile (Q4): 11.7%; Wilcoxon signed-rank test, $W = 21$, $p < 0.05$; Fig. 2.2b). The relative magnitude of FRic difference varied from 32.9% for Australia to 0.1% for Asia. Current FDis was consistently lower across continents, indicating increased similarity in species functional traits; FDis was lower both weighted by geographic range (-2.8%, Q2: 7.5%, Q4: 1.1%; $W = 21$, $p < 0.05$; Fig. 2.2c) and unweighted (-5.6%, Q2: 10.3%, Q4: 2.9%; $W = 21$, $p < 0.05$; Fig. 2c). The largest relative difference in FDis when weighted by geographic range occurred in Australia (42.2%). However, on average, we detected a near two-fold relative increase in FDis decline between the current and present-natural for the unweighted compared to weighted analysis. The reason for this was that the FDis-weighted centroids in the present-natural occurred in a species-rich location of trait space (causing a lower average distance from species) and shifted towards less species-rich locations. Alternatively, unweighted

centroids began in less species-rich locations (a higher average distance from species) and shifted to more species-rich locations of trait space, causing a greater negative difference in the FDis metric for the current ensemble. Analysis with systematically reviewed species showed similar trends (supplementary results), except for FDis difference in Europe, which increased when using unweighted FDis (Fig. A2.10), likely because almost all small insectivores were not systematically reviewed.

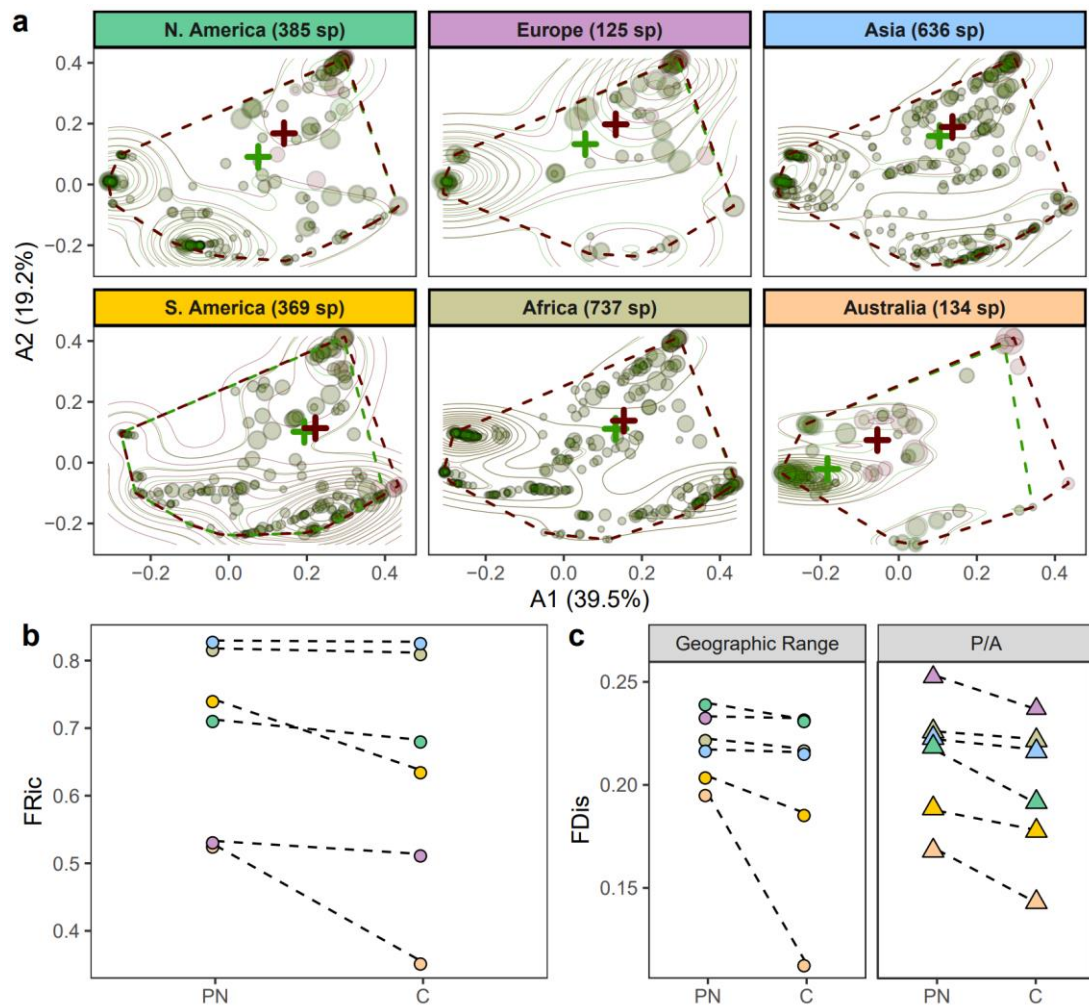


FIGURE 2.2 | Structural shifts and functional diversity differences of carnivorous mammal ensembles between the present-natural and current for each of the world's continents. (a) Continental functional trait spaces (species richness in parentheses) shown using the first two PCoA axes with species represented by points (size scaled to geographic range size) for present-natural (PN; brown) and current (C; green) ensembles. For simplicity, only the first two axes of change in functional richness are shown here by minimum convex polygons (dashed lines) for PN and C ensembles for each continent, explaining 59% of the variance, despite it being calculated from the first four axes. Functional dispersion is represented by the distance of all species from the ensemble centroids (crosses) representing the weighted centres of the functional hypervolumes, with the weight being species' geographic range size. (b) Differences in the 4-dimensional functional richness (FRic) for each continent between the PN and C ensembles. (c)

Difference in functional dispersion (FDis) between current and present-natural ensembles for each continent, calculated using two weighting methods: geographic range-weighted (left, circles) and presence-absence (P/A) only (right, triangles). Colours in b & c represent continents, colours as in a.

Comparing between present-natural and the current, continental ensemble centroids displayed similar directional shifts along axes in functional space (Fig. 2.2a & Fig. 2.3). The centroid shift magnitude was significantly different between the four functional trait axes for unweighted (Kruskal-Wallis: $\chi^2 = 18.75$, $df = 3$, $p < 0.001$) and weighted analyses ($\chi^2 = 17.62$, $df = 3$, $p < 0.001$). Continental ensembles shifted towards smaller-bodied and more insectivorous species, and away from hypercarnivorous species towards more herbivorous species, as indicated by shifts on A1 and A2, respectively.

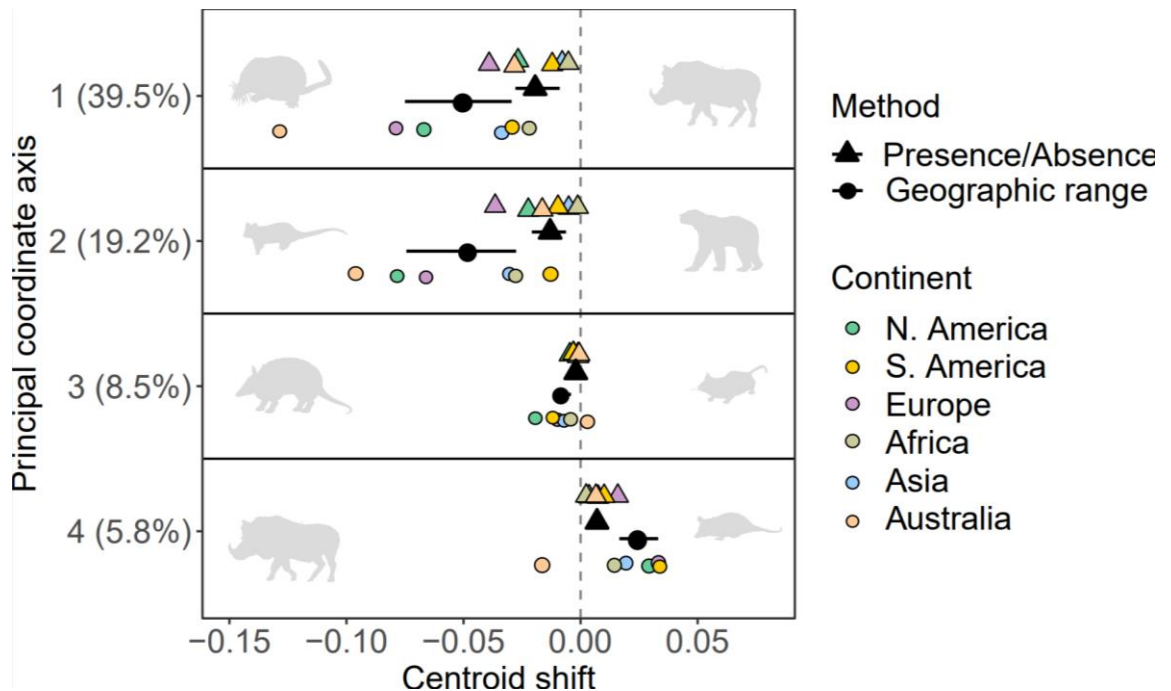


FIGURE 2.3 | The magnitude of structural shift of carnivorous mammal continental ensembles. The magnitude of continental ensemble centroid shifts between present-natural and current ensembles for each continent (coloured points) along the four PCoA axes of functional space (73% total variance). We used two different weighting methods: with geographic range (circles) and presence-absence only (triangles). Axis medians and interquartile ranges shown by black symbols and lines, respectively. Silhouettes highlight species at the extremes of functional space, including from high to low values: *Metridiochoerus compactus*[†] (extinct) to Alaska tiny shrew (A1), *Arctodus simus* (extinct) to long-tailed pygmy possum (A2), giant armadillo to montane African climbing mouse (A3), and gray four-eyed opossum to *Metridiochoerus compactus* (extinct) (A4). Negative shifts along A1 indicate shifts towards smaller species with more insectivorous diets. Negative shifts on A2 indicate shifts away from more carnivorous to more herbivorous species. Positive shifts along A3 indicate shifts away from larger-bodied

insectivorous species. Positive shifts along A4 indicate shifts away from large-bodied dietary specialists towards medium-bodied dietary generalists.

We detected a significant difference between the two weighting methods in the magnitude of the centroid shift along A1 (Mann-Whitney: $U = 5$, $p < 0.05$), and A2 ($U = 5$, $p < 0.05$), with geographic range weighting causing a 2.5-fold greater shift than using presence-absence only on A1, and 3.6-fold greater shift on A2. For systematically reviewed species there were, generally, shifts away from hypercarnivorous to more herbivorous species (A2). The exception was South America where ensembles shifted slightly towards hypercarnivores when using geographic range size as a weighting (Supplementary results; Fig. A2.11). A shift from larger-bodied to smaller-bodied species (A1) is still detected, although no significant difference between weighting methods. Similar results were seen on A3 and A4 compared to the full dataset, with geographic range weighted centroid shifts being greater on A3.

2.5 | Discussion

The global geographic ranges of carnivorous mammals are currently more reduced for species with greater body mass and with higher specialisation on vertebrate meat, as a result of late Quaternary extinctions and range contractions. This bias towards large-bodied, hypercarnivorous clades following ecological disturbance has been a common occurrence throughout mammalian evolution (Van Valkenburgh, 1999; Valkenburgh *et al.*, 2014). Trophic specialisation on large prey and intrinsic traits, such as low population densities, likely increases vulnerability of large-bodied hypercarnivores to ecological disturbances, such as the arrival of competitors (Van Valkenburgh, 1999; Valkenburgh *et al.*, 2014). This is analogous to the effects of modern humans which have competed with carnivores through prey exploitation (Ripple *et al.*, 2016), habitat modification (Canale *et al.*, 2012), and direct persecution (Ripple *et al.*, 2014). The loss of megafauna around the world (Smith *et al.*, 2018a) has reduced the diversity of resources for both predators and scavengers (Chamberlain *et al.*, 2005; Galetti *et al.*, 2018; Sandom *et al.*, 2018b). The selection against large, hypercarnivorous mammals is consistent with human-induced niche filtering (Balmford, 1996; Mouillot *et al.*, 2013), resulting in functional homogenization of carnivore ensembles globally (Clavel *et al.*, 2011). Despite diets having the potential to vary through space and time (Bojarska & Selva, 2012), our study

revealed continental ensembles have become increasingly ecologically similar as smaller-bodied, less carnivorous mammals have been more resilient to disturbances in the late Quaternary, a phenomenon predicted to continue into the future in response to anthropogenic pressures (Cooke *et al.*, 2019).

Despite range reductions of large-bodied, hypercarnivorous mammals having occurred across all continents, the magnitude of change varied. Australia suffered the largest relative decline in its carnivorous mammal ensemble, primarily because of the originally low functional redundancy of the continent's hypercarnivorous mammals. This was previously unreported because of taxonomic focus of research on Carnivora (Dalerum *et al.*, 2009). Furthermore, the loss of functional diversity for mainland Australia is likely underestimated because the only extant, native hypercarnivorous (100% vertebrate meat) mammal, the Tasmanian devil, is restricted to Tasmania. The native, highly-carnivorous tiger quoll, which still occurs on the mainland, also consumes a relatively high (30%) proportion of invertebrates. However, the dingo, an apex predator potentially introduced by humans, likely buffers the loss of functional diversity for the Australian ensemble (Letnic, Ritchie & Dickman, 2012b). In North America and Europe, ensembles have also suffered large structural shifts away from large-bodied and hypercarnivorous mammals, which was reflected in loss of functional richness and consistent with previous research (Dalerum, 2013). This may, in part, be explained by generally more research on these continents (Martin, Blossey & Ellis, 2012) and greater knowledge of species' range contractions. The South American ensemble experienced a large decline in functional richness, influenced by the loss of large-bodied, and primarily herbivorous, short-faced bears *Arctotherium tarijense* and *A. wingei*. The functional diversity and ensemble structure of carnivorous mammals in Asia and Africa have been less affected by late Quaternary extinctions. The large shift away from large-bodied hypercarnivorous species on continents would likely be even greater with wider taxonomic inclusion. In Australia, large-bodied, hypercarnivorous reptiles, including a large snake (*Wonambi naracoortensis*), monitor lizard (*Megalania prisca*), and terrestrial crocodile (*Quinkana sp.*), went extinct shortly after the arrival of modern humans (Roberts *et al.*, 2001). Including large scavenging birds whose range reduction was caused by the decline in megafauna carcasses in the landscape (Emslie, 1987), would further influence shifts in carnivorous species' functional diversity.

Geographic range contractions have been observed for a variety of taxa across the world (Ceballos, Ehrlich & Dirzo, 2017), with many extant carnivorous mammals having suffered large range contractions (Laliberte & Ripple, 2004; Wolf & Ripple, 2017). Our findings demonstrate that only considering extinction events, and not including geographic range size, likely leads to underestimates of ensemble structural changes at large spatial scales, although not necessarily changes in functional diversity metrics. This was particularly evident in the functional space axes relating to body mass and vertebrate consumption, which both had a roughly three-fold greater shift in the ensemble centroid position when weighted by geographic range compared to presence-absence alone. Shifts of this magnitude were expected for body mass because of the correlation between range size and body mass (Brown, Stevens & Kaufman, 1996); however hypercarnivory, alongside large body mass, was also another previously widespread functional trait that is now severely geographically restricted across continents. This may, in part, be influenced by the known, current range of large-bodied, hypercarnivorous species being smaller as they tend to have been studied in more depth (Brooke *et al.*, 2014), resulting in increased fragmentation and range loss (Table A2.5, and Fig. A2.12-13). However, such species are likely to have comparatively highly fragmented ranges in reality in response to anthropogenic pressures (Crooks, 2002; Newbold *et al.*, 2020). Although the lack of range reduction for small-bodied species is influenced by many not being systematically reviewed, this likely reflects reality because of the well described bias towards large body size extinctions during the Late Quaternary (Smith *et al.*, 2018a).

The shift of ensembles away from hypercarnivorous species across continents likely has global consequences for ecological processes. Predatory hypercarnivorous mammals have the potential to exert top-down forcing on prey populations both directly and indirectly (Ripple & Beschta, 2006; Ripple *et al.*, 2010; Estes *et al.*, 2011; Letnic *et al.*, 2012b; Malhi *et al.*, 2016), and influence the distribution of nutrients in ecosystems (Schmitz, Hawlena & Trussell, 2010). Removal of predators can lead to increased herbivore densities (Terborgh *et al.*, 2001) and cause mesopredator release (Prugh *et al.*, 2009). In Australia, removal of top-down forcing by apex predators has resulted in introduced mesopredators becoming abundant (Letnic & Koch, 2010), while the presence of apex predators has been shown to benefit native biodiversity (Wallach *et al.*, 2010). Reintroducing, or facilitating natural recolonization, of large predators may counteract these effects, with top-down effects demonstrated through herbivore behavioural changes

in response to grey wolves in Yellowstone National Park (Ripple & Beschta, 2004) and Europe (Kuijper *et al.*, 2013), the effects of predator auditory and scent cues on bushbuck in Mozambique (Atkins *et al.*, 2019), and the influence of dingoes on mesopredator populations in Australia (Newsome *et al.*, 2015). In Australia, reintroduction of the hypercarnivorous Tasmanian devil to the mainland could (re-)introduce top-down forcing on non-native mesopredators (Hunter *et al.*, 2015), although dingos are argued to already exert greater top-down pressures on mesopredators (Fillios, Crowther & Letnic, 2012) and capable of restoring the large predator guild (Newsome *et al.*, 2015). While these are active processes, restoring predator guilds could be achieved passively by promoting natural recolonization of predators, as seen in Europe (Chapron *et al.*, 2014), and incorporating management decisions to minimise human-carnivore conflict (Treves & Karanth, 2003). Although the range expansions of four species were excluded here, future research could assess the effects of such range changes, and include introduced species, to understand the full spectrum of continental ensemble functional change related to human-impacts.

The interacting effects of humans and changing climates throughout the late Quaternary have resulted in reductions in the current global ranges of large-bodied, hypercarnivorous mammals, compared to a counterfactual scenario in which humans had not migrated out of Africa. Range reductions have resulted in globally consistent structural shifts in continental carnivorous mammal ensembles, with the greatest loss of native functional diversity having occurred in Australia. While functional homogenization of carnivorous mammals will likely continue to occur in the coming century (Cooke *et al.*, 2019), we show that this process is already underway as continental ensembles have shifted towards smaller-bodied, less carnivorous species. We recommend enhanced protection of large-bodied, hypercarnivorous mammals, as well as identifying regions for facilitating natural recolonizations, reintroductions, and accepting already introduced apex predators, to reverse past attritions and preserve trophic complexity of current and future ecosystems.

CHAPTER 3 | Lost hypercarnivore functions could be partially reversed on most continents if predators could recolonise

“Nature does not hurry, yet everything is accomplished.”

Lao Tzu

3.1 | Abstract

Large hypercarnivores have been widely removed from ecosystems following human-induced extinctions and geographic range declines since the Late Pleistocene (LP; 130,000 – 11,700 years before present). Their removal has ensured the geographically widespread occurrence of herbivore and mesopredator populations being free from top-down pressures. As such, there are increasing calls to restore hypercarnivores to areas of their former geographic range to reinstate missing ecological functions. Natural recolonisations of extant hypercarnivores would contribute to these efforts but the extent to which they alone could reverse the effects of defaunation is unknown. To investigate this, we collated functional traits for all terrestrial, medium to large (>1kg) hypercarnivorous mammals that existed since the earliest LP ($n = 108$) and combined these with maps of species' (i) prehistoric geographic ranges, (ii) current-day geographic ranges, and (iii) potential geographic ranges today following maximised recolonisation. We show declines in functional diversity of continental hypercarnivore assemblages were generally no greater than expected from random extinctions but that large, pursuit predators have been lost to a greater extent than ambush predators relative to the number that have existed during the late Quaternary. Recolonizing hypercarnivores would buffer the loss of functional diversity across much of Eurasia, Africa, and North America. Large insular areas, including continental Australia, as well as South America would require alternative methods to restore missing ecological functions in hypercarnivore assemblages. We suggest that maximising landscape connectivity as a long-term

conservation goal would facilitate the passive restoration of missing ecological functions and increase the resilience of ecosystems.

3.2 | Introduction

The world's mammal assemblages have been severely defaunated following species extinctions and geographic range restrictions that coincided with the global spread of modern humans throughout the Late Pleistocene (LP; ~130,000 – 11,700 years before present, ybp) (Sandom *et al.*, 2014b). Defaunation was highly biased towards removing the largest herbivores and carnivores across the world's ecosystems (Smith *et al.*, 2018a). Hypercarnivores, species that depend upon vertebrate biomass ($\geq 70\%$ vertebrate meat in diet; Valkenburgh 1988) were most severely impacted of the carnivores were those with (Middleton, Scharlemann & Sandom, 2020). Some large hypercarnivores survived the LP extinction, though many remain threatened and confined to fragments of their former geographic ranges (Ripple *et al.*, 2014). A geographically widespread ecological legacy of these declines involves herbivore and mesopredator populations being free from top-down pressures that were once ubiquitous across the world (Ripple & Beschta, 2003; Winnie & Creel, 2017; Letnic *et al.*, 2011; Newsome *et al.*, 2017). Today, the subsequent ecological effects of herbivores and mesopredators are often framed as conservation problems, including woodland regeneration inhibition or high predation pressures on species of conservation concern (Hobbs, 2009; Ripple *et al.*, 2013; Woinarski *et al.*, 2015). To reverse these effects, remaining hypercarnivores could be restored to their former geographic ranges (Svenning *et al.*, 2016) but active efforts through translocations can be contentious (Nogués-Bravo *et al.* 2016). Passive restoration efforts would contribute to restoring hypercarnivore assemblages, but the extent to which they alone would reverse the effects of defaunation remains unknown.

Facilitating natural recolonizations by maximising landscape connectivity would passively contribute to the recovery of hypercarnivore assemblages (Perino *et al.*, 2019). Hypercarnivore recolonisations, including grey wolves (*Canis lupus*), pumas (*Puma concolor*), and Eurasian lynx (*Lynx lynx*), have widely occurred, and continue to occur, across Europe and North America (Berger, Swenson & Persson, 2001; Larue *et al.*, 2012; Chapron *et al.*, 2014) through a combination of land abandonment (Cimatti *et al.*, 2021) and carnivores having a better protection status than ~50 ybp (Chapron *et al.*, 2014; Smith

et al., 2014). In turn, prey behaviour and population dynamics has been influenced by recolonising hypercarnivores (Berger *et al.*, 2001), although such effects are likely to be context-dependent (Samelius *et al.*, 2013). For many hypercarnivores, recolonisations to their full former geographic ranges could be controversial as they often include areas far from their currently restricted geographic ranges (Faurby & Svenning, 2015; Wolf & Ripple, 2017). For example, spotted hyena (*Crocuta crocuta*), dholes (*Cuon alpinus*), and leopards (*Panthera pardus*) currently inhabit fragmented ranges across Africa and Asia but previously co-occurred across Europe in the LP (Rodríguez-Gómez *et al.*, 2012) and would likely still occur there if long-term effects of modern humans had been absent (Faurby & Svenning, 2015). Such palaeoecological insights are increasingly recognised as important for conservation (Barnosky *et al.*, 2017) and are even being incorporated into global conservation initiatives measuring species recoveries (Grace *et al.*, 2019). As such, it is timely to consider species' full potential geographic ranges, by taking insight from past geographic ranges, to maximise the restoration of ecologically downgraded ecosystems.

If hypercarnivores returned to their former geographic ranges, they could restore missing ecological functions that can have cascading effects in ecosystems (Ripple *et al.*, 2014). Alongside the numeric regulation of prey populations (Fillios *et al.*, 2010), hypercarnivores create predation risks across a landscape that can influence prey behaviour (Ripple & Beschta, 2004). The establishment and intensity of predation risk depends upon landscape structures and the composition of predator traits that govern how they hunt (Schmidt & Kuijper, 2015). A predator's body mass limits prey species it can interact with (Carbone *et al.*, 1999) while different hunting modes (e.g. ambush and pursuit) establish different intensities and distributions of predation risk (Schmitz, Krivan & Ovadia, 2004; Schmitz, 2008). As such, the influence of predator assemblages on the ecological dynamics of diverse prey assemblages will be influenced by the variety of hunting modes and body masses of predators that occur (Thaker *et al.*, 2011; Schmidt & Kuijper, 2015). Numeric regulation of deer has even been shown to be additive when hypercarnivores with different hunting modes co-occur (Ripple & Beschta, 2012b). Hypercarnivore assemblages in the LP consisted of diverse predators varying in body mass and hunting modes, but extinctions have reduced the variety of predator trait combinations in the world's ecosystems which has potential implications for the distribution of predation risk across landscapes (Dalerum *et al.*, 2009).

Here, we investigated how past defaunation modified hypercarnivore assemblage structures – measured using species richness, functional richness, and functional dispersion – and the extent to which natural recolonisations could reverse these changes. To do this, we collated a database of functional traits for all hypercarnivorous mammals that existed since the earliest LP and combined these with species’ geographic range maps. These geographic range maps included (i) species’ current-day geographic ranges and (ii) estimates of species’ geographic ranges today in a counterfactual scenario without the long-term effects of humans outside of continental Africa (henceforth ‘present-natural’). Present-natural geographic range maps are suitable proxies for the geographic ranges of species during the last interglacial period, during the earliest LP (~130,000), and comparing them to current-day maps can reveal long-term impacts of humans on the world’s mammal assemblages (Faurby & Svenning, 2015). To contextualise the severity of past extinctions at the continental-level, we analysed whether the loss of functional diversity was greater than expected from random species extinctions, and whether predators with certain hunting modes were disproportionately affected. We then created a third set of maps showing species’ potential geographic ranges today under a scenario of maximised recolonisation and investigated how past modifications could be reversed through recolonisations at (i) continental- and (ii) local-levels.

3.3 | Methods

3.3.1 | Hypercarnivore species list and their geographic ranges

We used the Phylogenetic Atlas of Mammals (PHYLACINE) database v1.2 for species selection (Faurby *et al.*, 2018). We selected all medium-large hypercarnivores ($n = 108$) that were mammal species $\geq 1\text{kg}$ and consume $\geq 70\%$ vertebrate meat (Valkenburgh, 1988) that has occurred since the earliest LP (~130,000 years ago).

For all medium to large hypercarnivores, we extracted two geographic range maps from PHYLACINE: present-natural and current-day ranges, both as rasters with a Behrmann equal-area projection and raster cell resolutions of 9000 km^2 . Present-natural ranges include counterfactual estimates of geographic ranges today in the absence of long-term impacts by modern humans (Faurby & Svenning, 2015). As present-natural ranges are estimates of mammal ranges in the current interglacial period, they are also suitable proxies for mammal ranges during the last interglacial occurring in the earliest

LP. To keep current-day ranges consistent and standardised with the production of the present-natural ranges, we used current-day range maps from Faurby & Svenning (2015) which are rasterized native ranges from the IUCN Red List Version 2016-3 (IUCN, 2016). To do this, the ‘*rasterise*’ function from the ‘*raster*’ package was used with any overlapping cells identified by setting the ‘*getCover*’ parameter to true. To validate the use of range maps, from 2016 we compared Version 2016-3 IUCN rasterised native range maps to Version 2021-3 IUCN rasterised native range maps to identify any changes in geographic ranges, including recolonisations that have happened during this time (Table A3.1). We created a third set of geographic ranges which reflected the potential area into which hypercarnivores could recolonise in the future under a scenario with maximised landscape connectivity. Specifically, these ranges consisted of the area hypercarnivores occupy in their present-natural ranges but restricted to the landmasses they occur on in the current-day.

3.3.2 | Functional traits

We selected six functional traits that can influence the ecological effects of predators. Functional traits included (i) average body mass ($\log_{10}$ -transformed; kg), (ii) ranked preferences of food types (mammal, plant, invertebrate, fruit, bird, herptile, fish: 0 = not-consumed, to 3 commonly-consumed), (iii) locomotion (ambulatory, scansorial, or cursorial), (iv) foraging habitat (terrestrial, arboreal, fossorial, or fishing), (v) hunting method (ambush, pursuit, or pounce-pursuit), and (vi) cooperative hunting ability (binary: 1 = yes, 0 = no).

Functional traits were collected from a variety of sources. Average body mass was available for all species from PHYLACINE v1.2 (Faurby *et al.*, 2018). Diet preferences were extracted from MammalDIET for all extant species (Kissling *et al.*, 2014). For extinct species, studies describing their diet were used and key words used to assign semi-quantitative values as in MammalDIET (e.g. ‘common’ prey would be assigned a 3 to that food type). Locomotion, hunting methods, foraging habitats and cooperative hunting were all extracted from a variety of sources identified from Google Scholar searches of species’ scientific names and the functional trait of interest. Papers that previously collated data for individual functional traits were extracted for all species available for that trait (e.g. locomotion in Samuels, Meachen & Sakai, (2013); hunting method in Valkenburgh (1985) and Dalerum (2013); sociality in Dalerum (2007) and Wallach *et al.* (2015)). If species were categorised as multiple options for each trait, they were assigned

to each of those categories. Evidence of cooperative hunting ability was searched for all species and a 1 assigned if observations had been made of their cooperative hunting ability. Except for lions, extinct species were assumed to be non-cooperative hunters as little evidence exists to support this. Group-living behaviour likely evolved before African lions (*Panthera leo*) expanded out of Africa and is thought to have persisted in American lions (*P. atrox*) and cave lions (*P. spelaea*) (Yamaguchi *et al.*, 2004). We therefore assigned extinct lions as cooperative hunters, despite American lions becoming genetically isolated from the other species of lion ~340,000 years ago (Barnett *et al.*, 2009). Additional sources of trait descriptions included species' IUCN Red List entries (IUCN, 2016) and the “*Encyclopedia of Mammals*” (Macdonald, 2006). Where species-level descriptions were unavailable, inferences from Genus- or Family-level has previously been done during the construction of other functional trait databases (Jones *et al.*, 2009; Wilman *et al.*, 2014).

3.3.3 | Statistical analyses

3.3.3.1 | Functional diversity of hypercarnivore assemblages

We first calculated pairwise Gower's distances between hypercarnivore trait compositions because traits were unequally weighted. As body mass correlates with many life history traits that influences species' ecologies, we weighted it by two, as in Lundgren *et al.* (2020). Categorical traits (e.g. locomotion) were separated into individual binary traits weighted by a proportion of the number of categories (e.g. cursorial, scansorial, and generalized were each weighted by 1/3). A principal coordinate analysis was performed on the Gower's distance matrix with a Cailliez correction for negative eigenvalues (Laliberté *et al.*, 2014). The first four principal coordinates were used for subsequent analysis (Maire *et al.*, 2015). We used the ‘*envfit*’ function in the R package ‘*vegan*’ (Oksanen *et al.*, 2013) to identify traits structuring the first two axes (hereafter ‘global hypercarnivore functional trait space’) using squared correlation coefficients (r^2).

Using species distributions within the global hypercarnivore functional trait space, two functional diversity metrics were calculated for hypercarnivore assemblages with the ‘FD’ package (Laliberté *et al.*, 2014), including functional richness and functional dispersion. While methods of measuring functional diversity vary greatly (Mammola *et al.*, 2021), the two functional diversity metrics were selected as, combined, they can reveal shifts in community structure following disturbances (Boersma, Kate *et al.*, 2016).

These were calculated at two scales: (i) continental-level, and (ii) raster cell-level, for each of the three geographic range maps: (i) the present-natural distribution of species, (ii) the current-day, and (iii) following recolonisations. Functional richness was calculated as the volume of the minimum convex hull of all hypercarnivores in an assemblage and describes trait composition diversity, varying from 1 (all predators present) to 0 (< 3 predators) (Villéger *et al.*, 2008). Functional dispersion was calculated as the average distance of hypercarnivores from assemblage centroids and describes average hypercarnivore dissimilarity (Laliberte & Legendre, 2010). As functional dispersion is sensitive to numeric weightings, we calculated continental-level functional dispersion for two weighting methods: (i) hypercarnivores weighted by their continental geographic range size and (ii) all hypercarnivores weighted equally (i.e. presence-absence).

3.3.3.2 | Null models of random species extinctions

To understand whether functional diversity was lost more than expected from random extinctions on continents during the late Quaternary, we compared functional diversity declines between actual and randomly assigned species extinctions. For each continent, we performed 1000 simulations whereby the same number of extinctions on a continent were assigned to random species occurring on that continent. We did not consider geographic range contractions at this step, so this analysis was performed using a single weighting method of presence-absence for functional dispersion. To investigate whether there was a significant difference between actual and random extinctions on continental functional diversity changes, we calculated whether actual functional diversity change occurred outside the 95% quantiles of simulated declines in functional diversity. This process was repeated for functional dispersion and functional richness separately.

To understand drivers of functional diversity declines, we investigated whether predators with certain hunting modes experienced relatively greater extinctions. To do this, we first performed a generalised logistic mixed-effects model with continent and taxonomic family as random effects. We used a hierarchical partitioning method for model selection by running models with each variable individually and with interactions, to identify the simplest model explaining extinction risk. We then performed a chi-squared test of independence (X^2) at the global-level to investigate specifically whether predators with certain hunting modes were lost disproportionately relative to the number that existed during the late Quaternary, which has implications for the capacity to restore

ecological functions that were removed following local and global extinctions. We performed a post-hoc comparison by looking at critical values of the residuals to a two-sided test following a Bonferroni correction, as performed in Schowanek *et al.* (2021). Following this, we tested whether predators with specific hunting modes had experienced larger range restrictions by performing a Kruskal–Wallis test on the number of cells lost between the present-natural and current ranges. A post-hoc Dunn test was used to identify pairwise differences between hunting modes.

3.4 | Results

Global and continental extinctions of hypercarnivorous mammals caused functional richness and functional dispersion to decline across the world's continents (Fig. 3.1). The first two axes of global hypercarnivore functional trait space (25% total variance explained) were structured by hypercarnivore body mass, locomotion, and hunting modes (Fig 3.1A). The third and fourth axes of functional trait space (11% variance explained) were structured by cooperative hunting abilities, body mass, and whether hypercarnivores are pounce-pursuit or pursuit hunters (Fig. A3.1). The greatest decline in functional richness occurred in Australia with a decline to zero because only two hypercarnivores remain. South America, North America, and Europe all suffered large declines, with just 5%, 37%, and 42% of LP functional richness remaining, respectively (see Fig. A3.2 for additional changes in functional space on axes 3 and 4). Africa and Asia still host 95% and 88% functional richness, respectively (Fig. 3.1B & C). Functional dispersion was reduced to a lesser degree, with the most to least impacted being Australia (28% of LP functional dispersion remaining), South America (71%), North America (89%), Europe (92%), Africa (94%), and Asia (96%).

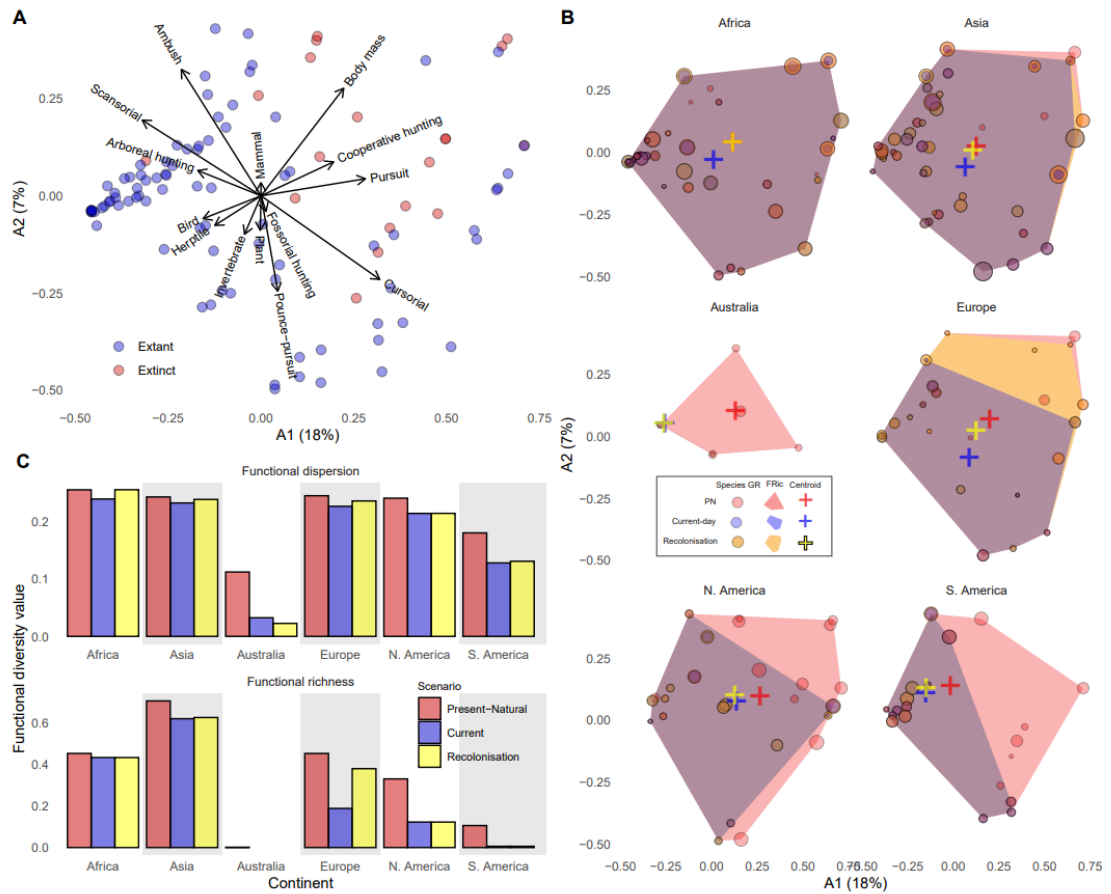


FIGURE 3.1 | Modifications to hypercarnivore assemblage structures from extinctions and range contractions and the recovery potential through recolonizations. (A) Global functional trait space (axes 1 and 2 only, axes 3 and 4 are in Fig. A3.2) showing the pair-wise dissimilarity of all extinct (red) and extant (blue) species (equally transparent and sized points) based on their functional traits. Arrows show individual traits scaled by their contribution to the structure of the global functional trait space. (B) Continental assemblages with points scaled by species' past (red), current (blue), and recolonized (yellow) geographic ranges sizes (GR). Polygons represent the functional richness of the past (red), current (blue), and recolonised (yellow) assemblages. Crosses indicate the geographic range-weighted assemblage centroids representing functional dispersion. (C) Functional dispersion (top) and functional richness (bottom) of each continental assemblage in the present-natural (red), current-day (blue), and following recolonizations (yellow).

Functional richness declines in hypercarnivore assemblages were more severe than expected from random extinctions only in South America, and functional dispersion in South America and North America (Fig. 3.1; observed decline < lower 95% quantile from 1,000 randomized extinctions). Asia and Europe both showed greater declines than the median randomized declines for both metrics, and North America for functional richness, but these were not significantly different from random extinctions.

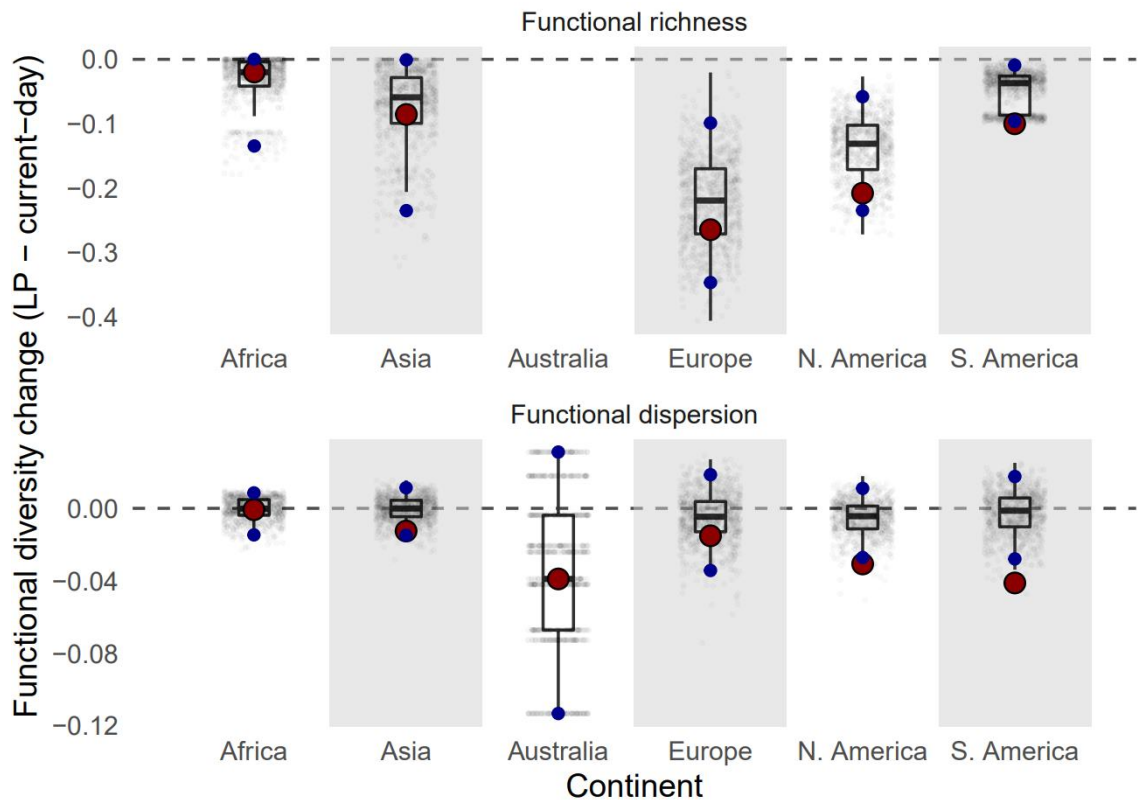


FIGURE 3.2 | Changes in continental functional diversity compared to randomized continental-level species extinctions. (A) Functional richness and (B) functional dispersion change following actual extinctions (red point) compared to 1000 random taxonomic extinctions simulations (transparent grey points). Australian change in functional richness is not shown as only two hypercarnivores remain in the current-day and so functional richness cannot be calculated. The same number of species extinctions from continents that occurred were assigned to random species and functional diversity calculated. Boxplots show the median, upper, and lower quartiles, as well as the maximum and minimum values shown by the whiskers. The upper and lower 95% quantiles of the distribution are indicated by blue points, with any changes following actual extinctions falling outside of this range being deemed as statistically significant.

Across continents, the best-supported model of extinction probability showed that body mass was the only trait that significantly influenced extinction risk (GLMM: $z = 5.05$, $p < 0.001$) with no detectable effect of hunting strategy influencing hypercarnivore extinctions probability. Yet, globally, we detected a relatively greater loss of pursuit hypercarnivores (32% pursuit hypercarnivores lost) (e.g. scimitar-toothed cats [*Homotherium latidens* and *H. serum*], dire wolves [*Canis dirus*], American cheetah [*Miracinonyx trumani*], extinct lions [*Panthera atrox* and *P. spelaea*]) compared to ambush predators (14% pursuit hypercarnivores lost) (χ^2 test of independence, $\chi^2 = 9.11$, $df = 2$, $p = 0.01$). However, pursuit predators (median body mass across species = 27kg) have also typically been characterised by larger body sizes throughout the Late

Quaternary than compared to predators with ambush (9.4kg) or pounce-pursuit (4kg) hunting modes (Kruskal-Wallis test: $\chi^2 = 15.06$, $df = 2$, $p = 0.002$; Fig. A3.4). The reduction in geographic distribution of predator hunting modes was also significantly different (Kruskal-Wallis test: $\chi^2 = 15.06$, $df = 2$, $p < 0.001$; Fig A3.3). A post-hoc Dunn test revealed pursuit predators (median range loss across species: 1105 cells) also lost a significantly greater geographic distributions than ambush predators (2 cells; Dunn test: $p < 0.001$) or pounce-pursuit (15 cells; Dunn test: $p < 0.001$).

At the continental-level, natural recolonizations would restore six hypercarnivores to Europe, two to Asia, and zero to other continents (Fig. 3.1B, C). The recolonisation of these new species would increase functional richness towards LP levels primarily for Europe (84% of LP levels; +42% from current-day) and slightly for Asia (89%; +1%). Within continents, the recolonisation of extant species to their former geographic range ensures functional dispersion, which is weighted by geographic range size, would increase most for Africa (100%; +6%), followed by Europe (96%; +4%), Asia (98%; +2.5%), and South America (73%; +2%). North America would see no change in functional dispersion. Australia's functional dispersion would decline further by 7% as only a single species, the tiger quoll (*Dasyurus maculatus*) would recolonise geographic range on the mainland which would shift the assemblage centroid towards it further.

At local scales, recolonizations would restore functional diversity and assemblage structures variably across continents (Fig. 3.3). Relative to LP levels, recolonizations would increase species richness and functional richness the most across assemblages in Europe, followed by Africa, Asia, North America, and South America (Fig 3.3A & B; Table 3.1). However, functional richness would be restored only very locally in South America. No functional richness would be restored through recolonisations in Australia. Functional dispersion would be restored most across Africa (Fig. 3.3C; Table 3.1), followed by Europe, Asia, North America, and South America. While the absolute change would be highest in Europe, the species richness and functional diversity that would be restored across Africa and Asia largely restores this to LP levels (Fig. S3.5-S3.7).

TABLE 3.1 | The average restoration by recolonisations at the local-level (raster cells) of metrics describing the structure of hypercarnivore assemblages. Values reflect the increase in metrics from hypercarnivore assemblages in the current-day (Fig. A3.5A-A3.7A) to those in a future recolonisation scenario (Fig. A3.5B-A3.7B), both relative to LP levels.

Median increase following recolonisations (%; LQ-UQ)			
	Species richness	Functional richness	Functional dispersion
Africa	31% (17-42%)	34% (8-71%)	9% (1-16%)
Asia	27% (14-40%)	22% (2-41%)	5% (0-8%)
Australia	0	0	0
Europe	46% (40-50%)	35% (25-39%)	6% (2-15%)
N. America	14% (0-20%)	15% (3-42%)	0% (0-9%)
S. America	0% (0-11%)	0% (0-6%)	0% (0-4%)

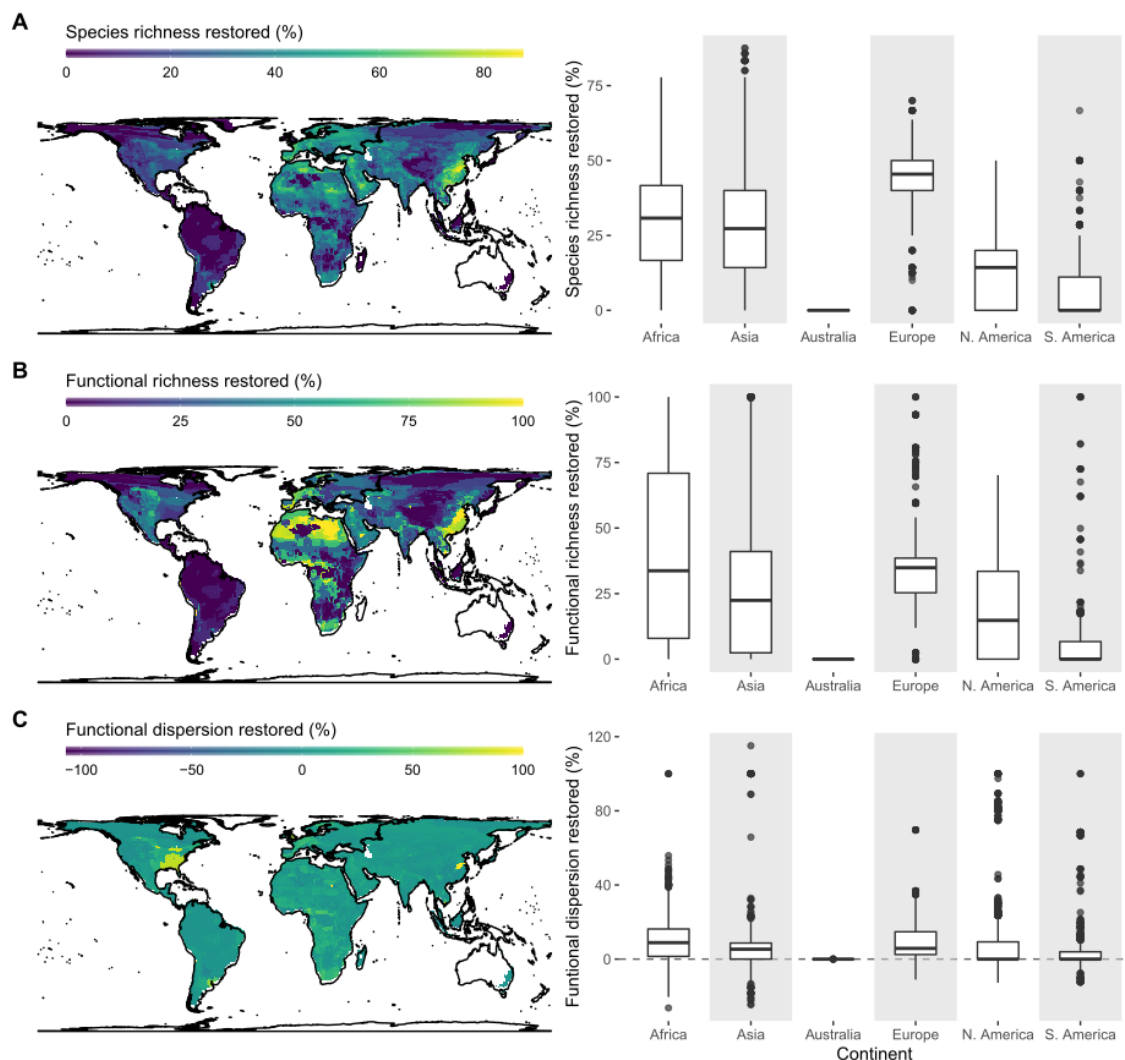


FIGURE 3.3 | Geographic variation in restoration opportunities for hypercarnivore assemblage structures through natural recolonisations. The difference in three community structure metrics between the current-day assemblages and a recolonisation scenario relative to LP levels. Metrics include (A) species richness, (B) functional richness, and (C) functional

dispersion, on a raster cell level (left-hand column). Bright colours on maps (shown with Behrmann equal-area projections) indicate a greater opportunity to restore assemblage structures. The separate values of current-day assemblage decline, relative to the LP, can be viewed in Fig A3.5-A3.7 for each metric, respectively. Boxplots indicate median, upper and lower quartiles. Whiskers indicate non-outlier minimum and maximum values. Outliers are points that are 1.5 times the interquartile range away from the upper or lower quartile.

3.5 | Discussion

Across most of the world's continents, hypercarnivore assemblage structures were severely modified by human-induced extinctions and range contractions during the Late Pleistocene (LP). Yet, if hypercarnivores could naturally recolonise their former geographic ranges, widespread opportunities exist to restore assemblage structures and missing ecological functions. As a result of few global extinctions, Africa and much of Asia would host hypercarnivore assemblages resembling the LP. Mainland Europe would see vast gains towards LP levels from hypercarnivores returning from refugia in Africa and Asia to their previously widespread European distributions, while others only occurred in the far-east or south-east, including African lions, cheetahs (*Acinonyx jubatus*), and tigers (*Panthera tigris*). Local regions in western Europe and North America would see benefits following the recolonisation of hypercarnivores that still occur on the continent but remain geographically restricted, including grey wolves and Eurasian lynx. In contrast, natural recolonizations in Australia and, to a lesser extent, South America, would do little to restore ecological functions that were lost following prehistoric and historic human-induced extinctions.

Recolonising large hypercarnivores would re-establish top-down pressures and predation risk for large herbivores and mesopredators that widely lack top-down pressures (Estes *et al.*, 2011; Ripple *et al.*, 2014). The loss of pursuit predators globally may have resulted in ecological legacies whereby predation risk has become more concentrated around closed-habitat edges from ambush predators that are more representative of assemblages across current-day ecosystems, as shown for pumas (Laundré & Hernández, 2003; Holmes & Laundré, 2006), Eurasian lynx (Podgórski *et al.*, 2008), and leopards (Balme, Hunter & Slotow, 2007). Restoring diverse forms of predation risk would contribute to reversing over-consumptive effects of herbivores and mesopredators which are commonly viewed as a conservation problem (Gompper, 2002; Mysterud, 2006; Mills *et al.*, 2020), particularly for recently introduced species (Vázquez,

2002; Woinarski *et al.*, 2015). Introduced herbivores restore ecological functions of herbivores driven extinct by humans and could restore past ecological dynamics and food webs if predators recolonised (Lundgren *et al.*, 2020). In North America, introduced donkeys restore ecological functions of extinct equids and their ecological effects are influenced by predation risk from pumas around closed habitats (Lundgren *et al.*, 2021a). Facilitating the recolonisations of cursorial pursuit predators where absent, such as grey wolves, could further the distribution of predation risk across open landscapes.

Natural recolonizations would require international efforts to maximise continent-wide landscape connectivity (Belote *et al.*, 2020). In fact, across Europe and North America, hypercarnivore recolonisations are already occurring following their improved protective status (Larue *et al.*, 2012; Smith *et al.*, 2014) and increased habitat availability (Cimatti *et al.*, 2021). While natural recolonizations have conservation benefits at the species- and ecosystem-levels, they are likely limited to longer-term conservation goals because range expansions can take considerable time, with wolves taking ~20 years to recolonise parts of Germany from neighbouring Poland (Reinhardt *et al.*, 2019). However, continent-wide range expansions have also been shown to occur relatively quickly, for example with golden jackals (*Canis aureus*) which have expanded their geographic range from the Balkans towards Switzerland and Estonia in ~50 years (Spasov & Acosta-Pankov, 2019). Recolonizations are also very unlikely for islands because of dispersal barriers. Increasing grazing pressures by deer populations free from top-down pressures across the United Kingdom is often cited as a cause of limiting widespread forest regeneration (Fuller & Gill, 2001). Yet, as it is separated from mainland Europe, recolonisation by large hypercarnivores are not possible. Alternatively, hypercarnivores restricted to insular refugia, such as the Tasmanian devil, would not be able to recolonise mainland ecosystems. In scenarios with dispersal barriers, reintroductions through active translocations are typically advocated for to restore top-down pressures on species at lower trophic levels (Hetherington, 2006; Nilsen *et al.*, 2007; Hunter *et al.*, 2015). As such, facilitating natural recolonisation will likely be a long-term conservation goal supplemented by reintroductions.

Regions where natural recolonisations and reintroductions would have limited impact would require alternative methods to restore missing ecological functions, such as the use of functional analogues (Donlan *et al.*, 2006). Recent research has shown that herbivores already present in ecosystems could restore ecological functions that were lost

following species extinctions, which is worth considering for other taxa (Lundgren *et al.*, 2020). In South America, lost ecological functions following dire wolf (*Canis dirus*) and sabre-toothed tiger (*Smilodon populator*) extinctions are irreplaceable by extant native species. Yet, feral dogs (*Canis familiaris*) restore an ecological function as group pursuit predators and, can influence the behaviour of prey as large as mountain tapir by hunting juveniles (*Tapirus pinohaque*) (Zapata-Ríos & Branch, 2016). However, feral dogs are also widely considered a threat to many species across South America (Doherty *et al.*, 2017a). To mitigate the ecological effects of feral dogs, natural recolonisations of jaguars and pumas could in turn re-instate top-down pressures (Butler *et al.*, 2014). In Australia, tiger quolls are the only remaining hypercarnivore on the mainland following the extinction of marsupial lions (*Thylacoleo carnifex*) and, more recently, thylacines (*Thylacinus cynocephalus*) and Tasmanian devils (*Sarcophilus harrisii*). The lack of apex predators is argued to cause negative ecological effects by red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) (Johnson, Isaac & Fisher, 2007), serving as a justification to reintroduce Tasmanian devils (Hunter *et al.*, 2015). However, dingoes already occur on mainland Australia and may arguably place greater top-down pressures on introduced mesopredators (Newsome *et al.*, 2015). Further, introduced herbivores might also be influenced by dingoes but the extent to which remains unknown (Forsyth *et al.*, 2018b).

Our recolonisation scenario explicitly assumed maximised landscape connectivity which is central to rewilding efforts through restoring degraded habitats and, where possible, removing anthropogenic dispersal barriers (Perino *et al.*, 2019). To achieve this, rural land management would need to be more accommodating of the presence of large predators, but this is argued to be possible at large regional scales at least across Europe (Merckx & Pereira, 2015). Recolonising hypercarnivores would, however, have socio-economic implications for livestock farmers (Smith *et al.*, 2014; Franchini *et al.*, 2021). To overcome these, supporting the uptake of predator-friendly farming methods may improve coexistence in the long-term (Johnson & Wallach, 2016). A further consideration is that, although conservationists often argue that hypercarnivore recolonisations would restore missing ecological functions (Ripple *et al.*, 2014), these may already be partly performed by humans (Norum *et al.*, 2015; Suraci *et al.*, 2019). In certain contexts, humans can drive prey behavioural modifications that exceeds that of non-human predators (Proffitt *et al.*, 2009; Ciuti *et al.*, 2012).

Restoring the structure of hypercarnivore assemblages would increase ecosystem resilience by either reinstating missing, or increasing the diversity of, ecological functions that influence top-down pressures in ecosystems. Natural recolonisations would offer widespread opportunities to restore hypercarnivore assemblage structures and the return of cursorial pursuit predators of open landscapes. However, many areas of the world, including relatively small (e.g. United Kingdom) and large (e.g. mainland Australia) islands, would require complimentary efforts through reintroductions or considering the acceptance of hypercarnivores that have recently established populations in novel ecosystems. Overall, we recommend international conservation efforts focus long-term efforts on maximising landscape connectivity and dispersal capacities to re-establish missing functional roles in ecosystems by enabling natural recolonisations.

CHAPTER 4 | CarniDIET: a global database on the diets of terrestrial, carnivorous mammals

“They say a little knowledge is a dangerous thing, but it’s not one half so bad as a lot of ignorance.”

Terry Pratchett

4.1 | Abstract

Motivation: A species’ diet is central to understanding many aspects of its biology, including its behaviour, movement, and ecological niche. The diets of terrestrial carnivorous mammals, defined here as species primarily consuming other mammals (hereafter, mammal-consumers), have been extensively studied and can vary in the proportion of different food types, and species, consumed across their geographic ranges. Accessibility to data capturing such variation in diets of mammal-consumers across the variety of ecosystems they occur in would provide valuable information for conservation, and open research avenues for macroevolution and macroecology. However, data on mammal-consumer diets across their geographic ranges have not been systematically collated. Here, we present CarniDIET (Version 1.0), an open-access database containing quantitative data on the diets of terrestrial mammal-consumers collated from the literature.

Main types of variable contained: Diet records capturing the percentage of mammalian prey, to the highest taxonomic resolution available, and non-mammalian food types (e.g. birds, invertebrates) in the diets of mammal-consumers at specific sites and times. Associated data with each diet record includes, where available, age and sex of mammal-consumer, sample size, sample origin, and quantification method as well as spatial and temporal variables including dates, season, study site, altitude and coordinates.

Spatial location and grain: Global, terrestrial. The spatial grain varies among sites from 0.03km² to 100000km², with a median of 170km². Study centroids are provided as latitude-longitude coordinates.

Time period and grain: Original diet samples were collected between 1933 and 2017, with half of studies collected between 1994 and 2008. Studies summarise diets from one month to 66 years, with a median of one year.

Major taxa and level of measurement: Terrestrial carnivorous mammals that primarily consume other mammals (103 species). Studies generally represent species' population averages, although can include demographic breakdowns.

4.2 | Introduction

A species' diet is central to understanding its biology, including its behaviour, movement and ecological niche (Simpson & Raubenheimer, 2012). Diet is defined as “the food(s) taken by members of a species over times ranging from one feeding period to periods over which fluctuations in the relative abundance of foods average out”, where ‘food’ refers to a “category of edible items which is a sensible grouping from the point of view of either predator or investigator” (Westoby, 1978). Diets therefore capture one-way consumptive trophic interactions which are influenced by individuals' nutritional requirements (Simpson & Raubenheimer, 2012) as well as abiotic and biotic factors (e.g. climate and competition, respectively).

Species-level representations of species diets commonly feature in functional trait databases (Jones *et al.*, 2009; Kissling *et al.*, 2014; Wilman *et al.*, 2014; Faurby *et al.*, 2018) used by macroecological studies across large spatial and temporal scales (Davis & Pineda Munoz, 2016; Middleton *et al.*, 2020). However, species often exploit a diversity of food resources (Pineda-Munoz & Alroy, 2014), making it challenging to summarise species' dietary strategies into categories, e.g. herbivore, omnivore, carnivore (Jones *et al.*, 2009). Some databases account for diverse diets by estimating global average compositional or semi-quantitative importance values for the species across multiple food categories (e.g. Kissling *et al.*, 2014; Wilman *et al.*, 2014). As species diets can vary at the population-level across space and time in the amount of different food types and prey species consumed, databases containing species-level globally averaged diet

compositions are limited in their utility to address questions at higher spatial and temporal resolutions.

A global database containing direct consumptive interactions identified for consumers across taxonomic groups exists ("GloBI", Poelen *et al.*, 2014), however it does not capture variation in a consumer's interactions, or its position in food webs, in space and time (Poisot, Stouffer & Gravel, 2015) or along environmental gradients (Tylianakis & Morris, 2017). Databases capturing spatial and temporal variation in trophic interactions are currently taxonomically restricted (e.g. felids, Sandom *et al.*, 2017; reptiles, Grundler, 2020). Therefore, compiling standardised quantitative interaction data across multiple taxonomic groups will enable predictions of species' interactions under future environmental changes (Agrawal *et al.*, 2007; Tylianakis & Morris, 2017) and aid conservation (Tylianakis *et al.*, 2010; Akçakaya *et al.*, 2018) by enabling better assessments of species' resource requirements and functional recoveries (Brodie, Redford & Doak, 2018; Akçakaya *et al.*, 2020).

Many large, terrestrial carnivores – some of which are threatened with extinction – are capable of exerting top-down pressure in ecosystems (Ripple *et al.*, 2014), increasing calls for reintroductions to restore top-down interactions (Svenning *et al.*, 2016). The combination of vulnerability and top-down effects in ecosystems suggests there is a timely need for open-access quantitative data on spatial and temporal variation in carnivore diets to identify resource requirements, predict ecosystem impacts (Baker *et al.*, 2017), and assist with recovery assessments (Akçakaya *et al.*, 2020). Previous diet studies on carnivores have investigated the effects of intra-guild competition (e.g. Carvalho & Gomes, 2004), anthropogenic pressures (e.g. Henschel *et al.*, 2011), altitude (e.g. Green, 2003), seasonality (e.g. Stenseth *et al.*, 2016), and local ecology (e.g. Vlachos, 1994). Such studies have been combined to address conservation questions about individual carnivore prey preferences (Hayward & Kerley, 2008) and diet variation across abiotic gradients (Virgos *et al.* 1999, Bojarska & Selva 2012), and to conduct multi-species macroecological and macroevolutionary analyses. However, such analyses are often taxonomically and morphologically limited, such as vulnerability of felids to prey loss (Sandom *et al.*, 2017) or dietary breadths of large (> 14.5kg) Carnivora (Ferretti *et al.*, 2020). Collating and making openly accessible diet data across taxonomic groups of carnivorous mammals across wider body mass ranges would allow further conservation

questions to be answered and open research avenues in macroevolution and macroecology.

Here, we present CarniDIET 1.0, an open-access database collating quantitative data on population-level diets of terrestrial carnivorous mammals from the literature.

4.3 | Data collation

4.3.1 | Species selection

All mammal species selected were extant, terrestrial (excluding cetaceans, pinnipeds, and sirenians), and reported to consume other mammals as a primary food type from MammalDIET (i.e. Mammals coded as 1 in Kissling *et al.* (2014); 208 species). MammalDIET contains species-level, globally-summarised (i.e. not population-level data), semi-quantitative diet preferences of mammals for broad food categories (e.g. mammals, birds) based on qualitative data from the IUCN Red List (IUCN, 2016) and Nowak (1999). To follow Phylacine 1.2 taxonomy (Faurby *et al.*, 2018), a database built for macroecological analyses of mammals during the late Quaternary, we excluded three species, now recognised synonyms, from the MammalDIET-derived species list. We also added five species absent from the MammalDIET-derived species list (*Felis bieti*, *Herpestes auropunctatus*, *Leopardus guttulus*, *Mustela russelliana*, *Mustela tonkinensis*) that were split from another mammal-consumer species. Hereafter, we refer to these species (210 species) as ‘mammal-consumers’.

4.3.2 | Diet data sources

Building upon a previous database of felid diets (FelidDIET, Sandom *et al.*, (2017)), we searched, following the FelidDIET protocol, the Clarivate Analytics Web of Science Core Collection (WoS; Version 5.3, 1864-March 2019) for sources on non-felid mammal-consumer diets. For felids, we searched for additional sources published since 2017 when FelidDIET was released. Sources were identified as peer-reviewed papers returned from WoS searching the ‘Topic’ field with: Species scientific name AND “diet”. From this initial list, we excluded sources that: (1) were unavailable as PDFs, (2) were not investigating species’ diets, (3) only reported qualitative data, or (4) focused on interactions with a specific prey species. For sources that presented diet data collected from another potential source, the potential source was included if available as a PDF.

4.3.3 | Data extraction

Data were systematically extracted from sources (Fig. A4.1) into Microsoft Excel (Microsoft Office 365, Version 2002). For each source, we recorded the author(s), journal, publication title, and publication year. Each source contains a number of ‘diet records’, with a single diet record represented by a single row in CarniDIET. A diet record is the percentage of a single mammalian prey species, or mammalian prey taxa at the highest taxonomic resolution, or sum for each non-mammalian food type (e.g. birds, invertebrates; see metadata for number of levels of other non-mammalian food types), in a mammal-consumer’s diet alongside additional data describing the methods used to quantify the diet record as well as spatial and temporal information. A ‘study’ within a source represents a series of diet records describing a mammal-consumer’s diet to the highest demographic and geographic resolution (Fig. A4.2) that employs one or more diet sampling protocols (e.g. scat collection) or quantification methods (e.g. frequency of occurrence) across: (1) one season or year, or averaged across multiple years or seasons (single composition); (2) multiple-seasons across one, or averaged, years (seasonal comparisons); (3) one, or averaged, seasons across multiple years (time-series); or (4) multiple-seasons across multiple-years (seasonal comparison time-series). The sample size of the sampling protocol(s) was recorded if reported in the source. For pre-2017 sources on felids, we collected additional variables absent from FelidDIET (e.g. sex).

Spatial and temporal data for studies were collated to the highest resolution reported within the source. Sources reported spatial and temporal data inconsistently, and we only recorded information provided in the source. Spatial data included location description, coordinates, and study area size. Location descriptions follow Darwin Core standards (Wieczorek *et al.*, 2012). If coordinates were not reported, we extracted coordinates from Google Maps for the centroid of the highest resolution spatial description reported. Coordinates extracted from Google Maps should be considered less precise than those reported in sources. Study area size (km²) was recorded when reported in the source. Temporal data included start and end years, months and days, and the reported season the study covered.

Diet records were extracted from tables, figures, text, and/or supplementary material of sources and the basis from which data were extracted from each source was recorded (e.g. Table). The methods used to quantify diet records, including sampling protocol and quantification method, were extracted (definitions in metadata). Common

and/or scientific names of mammalian prey species were recorded. Any missing common or scientific names of prey were added using common and scientific name pairs from other sources in CarniDIET that provided both or looked up in the IUCN Red List. Prey scientific names were standardised to the Phylacine taxonomy, including prey synonym updates and sub-species given at the species-level. For domesticated species, we included scientific names (e.g. *Bos taurus*), despite these species not being included in Phylacine.

4.3.4 | Data validation

We randomly selected 5% of sources (37 sources) and compared diet records in CarniDIET to the original source. Accuracy in percentage values for diet records in CarniDIET were checked and any missing diet records identified.

4.4 | Results

The species selection criteria returned 210 potential mammal-consumers from 9 orders and 23 families. We found quantitative diet studies for 103 mammal-consumers across 5 orders and 15 families. The number of mammal-consumers with quantitative diet studies varied between families (Table A4.1; Fig. A4.3), with Felidae (n = 29 species; 83% of possible mammal-consumers in the family), Canidae (22; 81%) and Mustelidae (18; 47%) having the highest number of species with diet studies. We found diet studies for all mammal-consumers within three families (Hyaenidae, Procyonidae and Ursidae), although these families include few mammal-consumers (≤ 3 species). Three families include high numbers of mammal-consumers (Didelphidae: 26 species; Viverridae: 22; Dasyuridae: 19) but, compared to other families with mammal-consumers, are relatively under-represented in dietary studies ($\leq 37\%$ possible mammal-consumers in each family studied).

Data were extracted from 719 sources containing 1,310 studies spanning 84 years (1933-2017; Fig. 4.1a), resulting in 29,121 diet records. Studies were conducted mostly in recent years (median = 2001; interquartile range: 1994-2008) summarising diets for one year (median, range from one month to 66 years). The spatial grain (km²) varied among sites from 0.03km² to 100000km², with a median of 170km². Studies were spatially concentrated in Europe, southern Africa, non-Amazonian South America, North America and South-Eastern Australia (Fig. 4.1b) which do not necessarily reflect high mammal-consumer species richness (Fig. A4.4-5). Of the studies, 15% are seasonal

comparisons, 4% are time-series, 5% are seasonal comparison time-series, and 76% report single diet compositions.

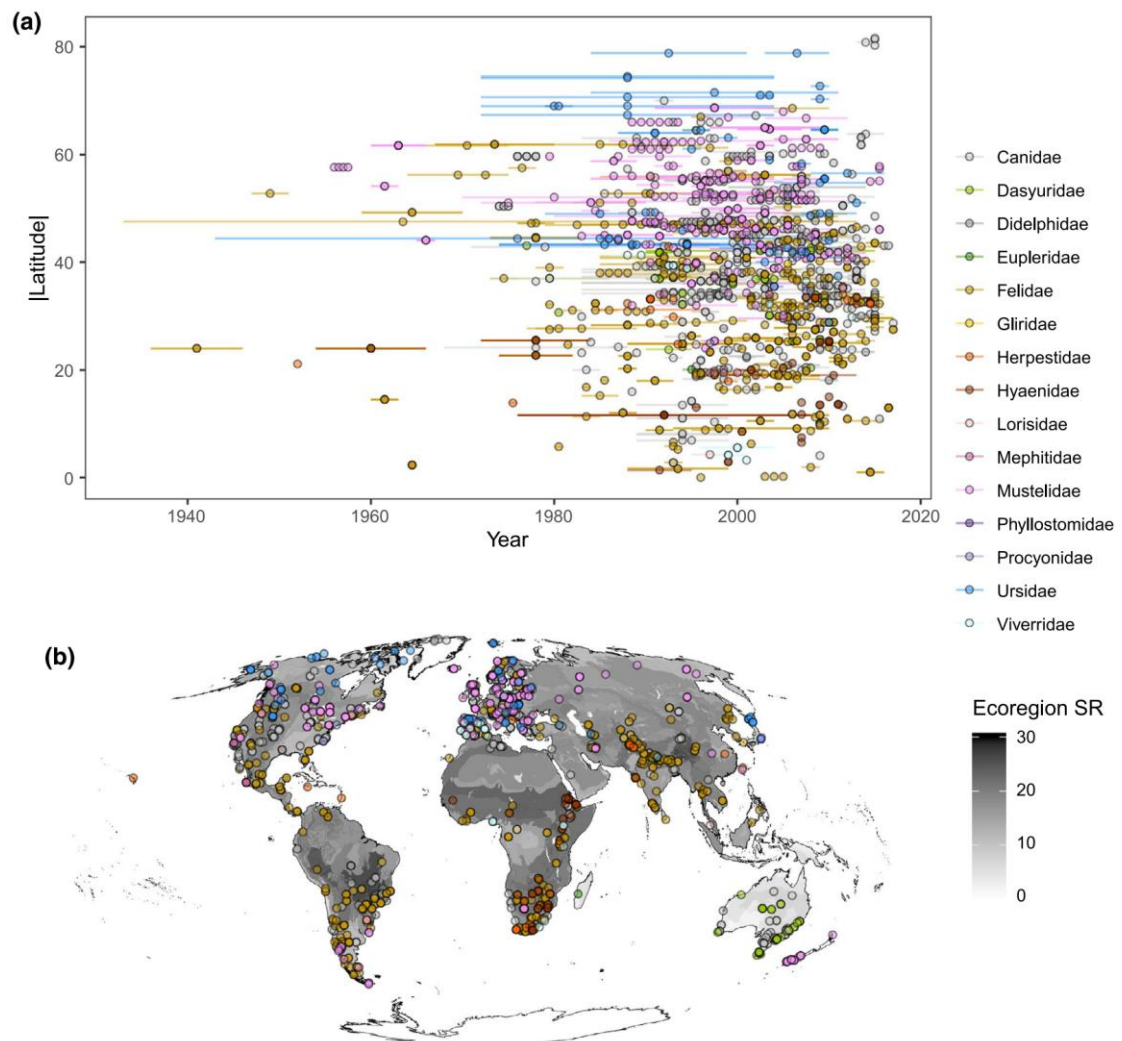


FIGURE 4.1 | Spatial and temporal distribution of mammal-consumer diet studies within CarniDIET. (a) Temporal duration and absolute latitude of studies. Points (equal-transparency with overlapping points creating darker colours) indicate mid-years and lines start and end years of studies. Time-series of diet studies from the same source are indicated by adjacent points with identical absolute latitudes. (b) Spatial distribution of studies, with mammal-consumer species richness (darker shades of grey indicate higher mammal-consumer species richness ('SR' in legend)) shown for each ecoregion (Olson *et al.*, 2006). Map shown in Mollweide equal-area projection. For both (a) and (b), point colour indicates family membership.

The number of sources and studies were unevenly distributed across mammal-consumers (Fig. 4.2a). Red foxes (*Vulpes vulpes*) were the most studied mammal-consumer (168 studies from 91 sources), contributing 12% of studies (Fig. A4.6). The five most studied mammal-consumers (red fox; grey wolf, *Canis lupus*; leopard, *Panthera*

pardus; puma, *Puma concolor*, coyote, *Canis latrans*) contributed 32% of all studies, and the 12 most-studied 50% (Fig. A4.6).

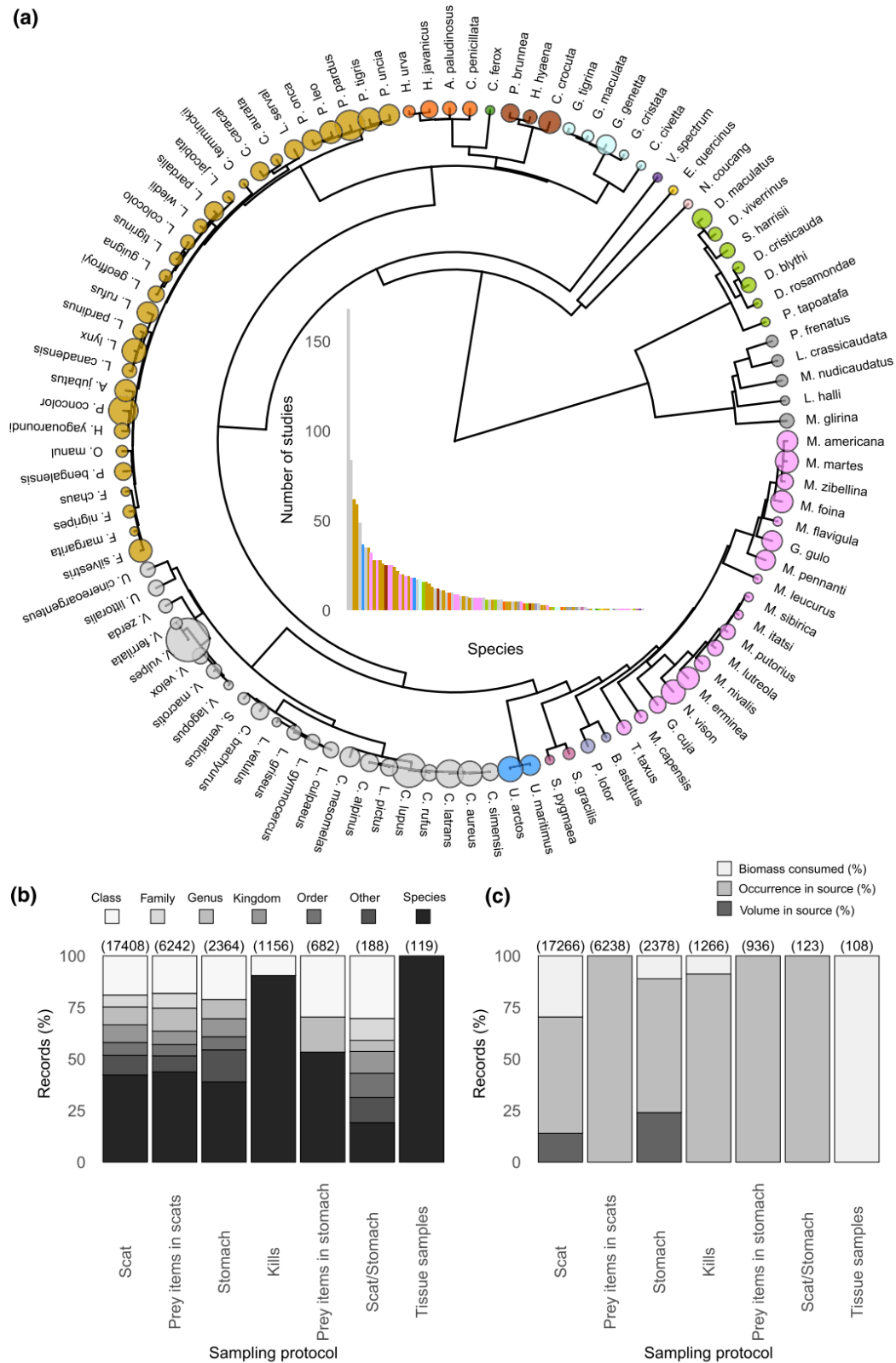


FIGURE 4.2 | Taxonomic and methodological coverage of the data stored in CarniDIET Version 1.0. (a) Phylogeny (Faurby *et al.*, 2018) of 103 mammal-consumers with diet studies in

CarniDIET from 15 families (coloured, transparent points) with the number of diet studies for each species shown by size of point, and shown in the inset barplot (colours indicate families, ordered from most to least studied species). Information for all potential mammal-consumers (210 species) is available in the supplementary material (Fig. A3.7). The percentage of diet records from each sampling protocol where food types were recorded to different taxonomic precision (b) and by different diet quantification methods (c). Number of records for each sampling protocol are shown in parentheses, with different numbers a result of combinations of sampling protocol and (b) taxonomic resolution, or (c) quantification methods. Combinations with >100 records shown, representing the majority of diet records; all combinations are shown in Figure S8-9.

Taxonomic resolution of diet records varied throughout CarniDIET (Fig. 4.2b). Species-level diet records were the most common (43%), followed by class (18%), and genus (9%). A total of 853 prey species, including domesticated animals, were recorded in CarniDIET. Of the species-level records, even-toed ungulates were most commonly reported (37% of the species-level records), followed by rodents (31%), and carnivores (11%). Diet records were mostly sampled from scats (60%; Fig. 4.2b, c), prey items in scats (22%), or stomachs (8%). Diet records were mostly quantified from occurrence in sampling protocol (69% records; Fig. 4.2c), followed by biomass consumption (20%) and volume in sample origin (10%).

Data-validation found that 97% of values in diet records matched the original source, indicating high accuracy. Of the mammal diet records, 1.2% were not identified correctly to species-level, and in 3% of sources one species-level diet record was missed. Additional diet records were missed from CarniDIET (50% missed records from one source), as a result of a missed quantification method, sampling protocol, or yearly breakdown from 5 re-assessed sources.

4.5 | Discussion

The first release of CarniDIET is the most comprehensive open-access database of quantitative diet data of terrestrial, carnivorous mammals that primarily consume other mammals. Inspired by a database on felid diets (Sandom *et al.*, 2017), we demonstrate the capability of developing such a database by increasing taxonomic scope, food types included, and additional metadata. As a result of a limited source search criteria, we acknowledge CarniDIET 1.0 is not a comprehensive resource of all dietary studies but we aim to continue developing CarniDIET in the future.

The taxonomic and geographic extent of data in CarniDIET highlights knowledge gaps and limitations in data-availability to prioritise future research (Bezanson & McNamara, 2019). Taxonomic bias is evident with >50% of studies in CarniDIET focussing on one of twelve mammal-consumers out of a possible 210. Small-bodied mammal-consumers, including carnivorous marsupials (Dasyurids and Didelphids) and mainly tropical Old World families of Carnivora (Viverridae and Herpestidae), are generally under-represented which is a known bias in carnivore research (Brooke *et al.*, 2014). The geographic distribution of studies follows trends in other macroecological databases (e.g. Salguero-Gómez *et al.*, 2016; Santini *et al.*, 2018), not necessarily reflecting areas of high mammal-consumer species richness. Furthermore, studies can be unevenly distributed across species' geographic ranges and understanding the implications of this could be a future research avenue. Future data collation should consider non-English language sources (Konno *et al.*, 2020) and utilise other databases (e.g. Zoological Record) which may reduce geographic and taxonomic biases.

Analyses using macroecological datasets should account for sampling methods (Santini *et al.*, 2018), which can be done with CarniDIET. Sampling protocols of diet studies have their own biases, whereby prey item identification (e.g. hairs) in scats and stomachs can overestimate small-bodied prey consumption (Steenweg *et al.*, 2015) while observed kills underestimate small-bodied prey consumption despite reflecting absolute number of prey consumed (Tambling *et al.*, 2012). Further, quantification methods provide different information on species' diets, and using more than one method is recommended to overcome limitations in each (Klare, Kamler & MacDonald, 2011).

Other species not included in CarniDIET, for example species of birds and reptiles, are also carnivorous and primarily consume mammals, and future data collation could increase the taxonomic scope to gain more complete food webs (Maiorano *et al.*, 2020). Future collation should also consider incorporating higher resolutions of non-mammalian food types. However, the availability of quantitative trophic interaction data is timely for terrestrial mammalian carnivores for applied conservation projects, as many are threatened (Ripple *et al.*, 2014), for recovery assessments, reintroductions, and trophic rewilding projects (Svenning *et al.*, 2016; Akçakaya *et al.*, 2018, 2020). Further, collation of site-specific quantitative diet data in CarniDIET increases data availability for macroecological studies investigating ecological interactions across varying environments and under future global changes.

CHAPTER 5 | Evidence-based trophic rewilding is geographically limited by contextually biased knowledge of species interactions

“When an ecologist says ‘there goes a badger’ they should include in their thoughts some definite idea of the animal’s place in the community to which it belongs, just as if they had said ‘there goes the vicar’.”

Charles Elton

5.1 | Abstract

Species reintroductions are central to trophic rewilding and are predicated on understanding how species interact. However, species interactions are influenced by environmental contexts, the abiotic and biotic conditions of the environment, creating concerns about unanticipated outcomes from trophic rewilding. Such concerns could be addressed through evidence-based predictions of reintroduction outcomes by using species trophic interactions observed from environmental contexts resembling the reintroduction area. We investigated the geographic scope for such evidence-based predictions for 43 extirpated carnivores using an open-access database of their interactions. We found geographically widespread opportunities for evidence-based predictions, but vast areas across species’ potential and current geographic ranges that have environmental contexts still to be studied. Species’ geographic ranges were also represented less than expected given study effort, indicating knowledge of species interactions tend to originate from similar environmental contexts. We recommend the future study of species interactions across broader geographic scopes to better inform in-situ conservation and trophic rewilding.

5.2 | Introduction

To reverse widespread ecosystem degradation the United Nations have proclaimed 2021 to 2030 as the Decade on Ecosystem Restoration. As part of this, trophic rewilding has been proposed as a key requirement to re-establish self-regulating and biodiverse ecosystems through restoring trophic complexity (Fernández *et al.*, 2017; Perino *et al.*, 2019; Svenning, 2020). This would involve reintroducing extirpated species to reinstate their top-down interactions that influence the structure and functioning of ecosystems (Svenning *et al.*, 2016). However, a commonly raised concern is the risk of unanticipated ecological outcomes (e.g. Nogués-Bravo *et al.* 2016). To overcome this concern, prior knowledge of species' interactions could help predict the potential ecological outcomes of their reintroduction (IUCN/SSC, 2013; Baker *et al.*, 2017; Pires, 2017). However, species interactions are influenced by abiotic and biotic conditions of the environment (hereafter 'environmental context') in which they occur (Wallach *et al.*, 2015b; Early & Keith, 2019), which vary across their geographic range (Maron, Baer & Angert, 2014; Haswell *et al.*, 2017; Wirsing *et al.*, 2020). As such, the breadth and strength of unanticipated interactions that establish from a reintroduced population in their newly re-occupied homes may be hard to predict.

Predicting the outcomes of species reintroductions would be more accurate when knowledge of their interactions is used from areas with comparable environmental contexts. Such context-specific knowledge would be considered as highly relevant in conservation decision-making (Christie *et al.*, 2020) and would likely ensure more accurate predictions of reintroduction outcomes (Pires, 2017). Observations from more dissimilar environmental contexts, and therefore of lower relevance, would also provide valuable information on the resources a species consumes, but may not reflect ecologically important interactions that may be context-dependent (Early & Keith, 2019). Assessing the extent that studies on species interactions represent the environmental contexts across their potential geographic ranges (i.e. areas of their former range and that could be areas of reintroduction) would therefore reveal the geographic scope for evidence-based trophic rewilding using knowledge of high relevance (Britnell *et al.*, 2021). Such assessments could further reveal bias in the environmental contexts that have been researched, which may skew our perceptions of species' ecologies (e.g. Mengüllüoğlu *et al.* 2018) and potentially increase risks of unanticipated ecological outcomes from trophic rewilding.

Carnivores are often considered as reintroduction candidates for trophic rewilding projects because they can establish top-down forces in ecosystems (Ripple *et al.*, 2014) and because they experienced widespread extinctions and local extirpations since prehistory (Middleton *et al.*, 2020). Many carnivore species have also been studied extensively across their geographic ranges, which would suggest that opportunities exist for evidence-based trophic rewilding (Brooke *et al.*, 2014). Dietary studies, in particular, could be used to predict reintroduction outcomes because they describe the direct trophic interactions a predator could establish in a given area (Baker *et al.*, 2017; Pires, 2017). However, carnivore diets can vary across their geographic ranges (Bojarska & Selva 2012; Díaz-Ruiz *et al.* 2013), suggesting the environmental contexts of study areas would need to be considered when predicting the outcomes of carnivore reintroduction.

Here, we investigated the extent to which the geographic ranges of extirpated carnivores are represented by the environmental contexts of existing diet studies, as well as where future study efforts could facilitate further representation. Environmental contexts were measured as the unique combination of five quantitative environmental variables that can influence a carnivore's resource selection in an area (Table S1) (Ellis *et al.* 1976), although we present results when two and five environmental variables are used to reflect environmental contexts that are characterized at low and high levels of complexity. We use two species as case-studies to exemplify our approach, grey wolf (*Canis lupus*) and dhole (*Cuon alpinus*). We then tested whether the distribution of species' diet studies, and the environmental contexts they are associated with, creates a biased representation of their geographic ranges. In doing so, we identified how well existing knowledge of species interactions represent their potential geographic ranges today, and therefore of the geographic scope for future evidence-based trophic rewilding.

5.3 | Methods

5.3.1 | Potential geographic ranges of extirpated carnivores

We established a species list of terrestrial carnivorous mammals that primarily consume other mammals and have quantitative interaction data available from an open-access dataset ($n = 103$; Middleton *et al.* 2021). Of these, we identified extirpated carnivores (i.e. carnivores that do not currently occupy their potential geographic range today because of former human-induced local extinctions) that could be reintroduction candidates as species not occupying their potential geographic range today following prehistoric, historic, and ongoing human impacts ($n = 43$ species). The potential ranges of these species were taken as the ‘present-natural’ maps of PHYLACINE v.1.2, which are estimates of mammal ranges today in the absence of long-term modern human (*Homo sapiens*) impacts outside of continental Africa (Faurby & Svenning, 2015; Faurby *et al.*, 2018). Species current geographic ranges were IUCN range maps and are nested within their potential ranges (IUCN, 2016). Species selection, and all following analyses, were performed in R v. 3.6 (R Core Team).

5.3.2 | Environmental niche breadths

We refer to the range of unique combinations of abiotic and biotic conditions (i.e. ‘environmental contexts’) of areas across species’ geographic ranges as their environmental niche breadth (Gaston, Blackburn & Lawton, 1997). We initially selected five abiotic and four biotic variables that could influence a species’ diet (Table A5.1) and standardised these as global raster layers with a resolution of 50km x 50km cells (henceforth an ‘area’). To limit autocorrelation among environmental variables, we proceeded with mean annual temperature, rainfall seasonality, elevation, mammal species richness, and human influence index. Environmental variables were standardised by scaling and zero-centering with the ‘scale’ function.

To measure environmental niche breadths, we used the ‘hypervolume’ package to construct multi-dimensional hypervolumes (Blonder & Harris, 2018). We extracted the environmental variables from areas within each species’ potential geographic range and their combination was used to describe the area’s environmental context. Using the environmental contexts for each species’ current and potential geographic range, we constructed their potential and current environmental niche breadth hypervolumes using multidimensional hyperbox kernel density estimations (KDE) (Blonder *et al.*, 2014). We

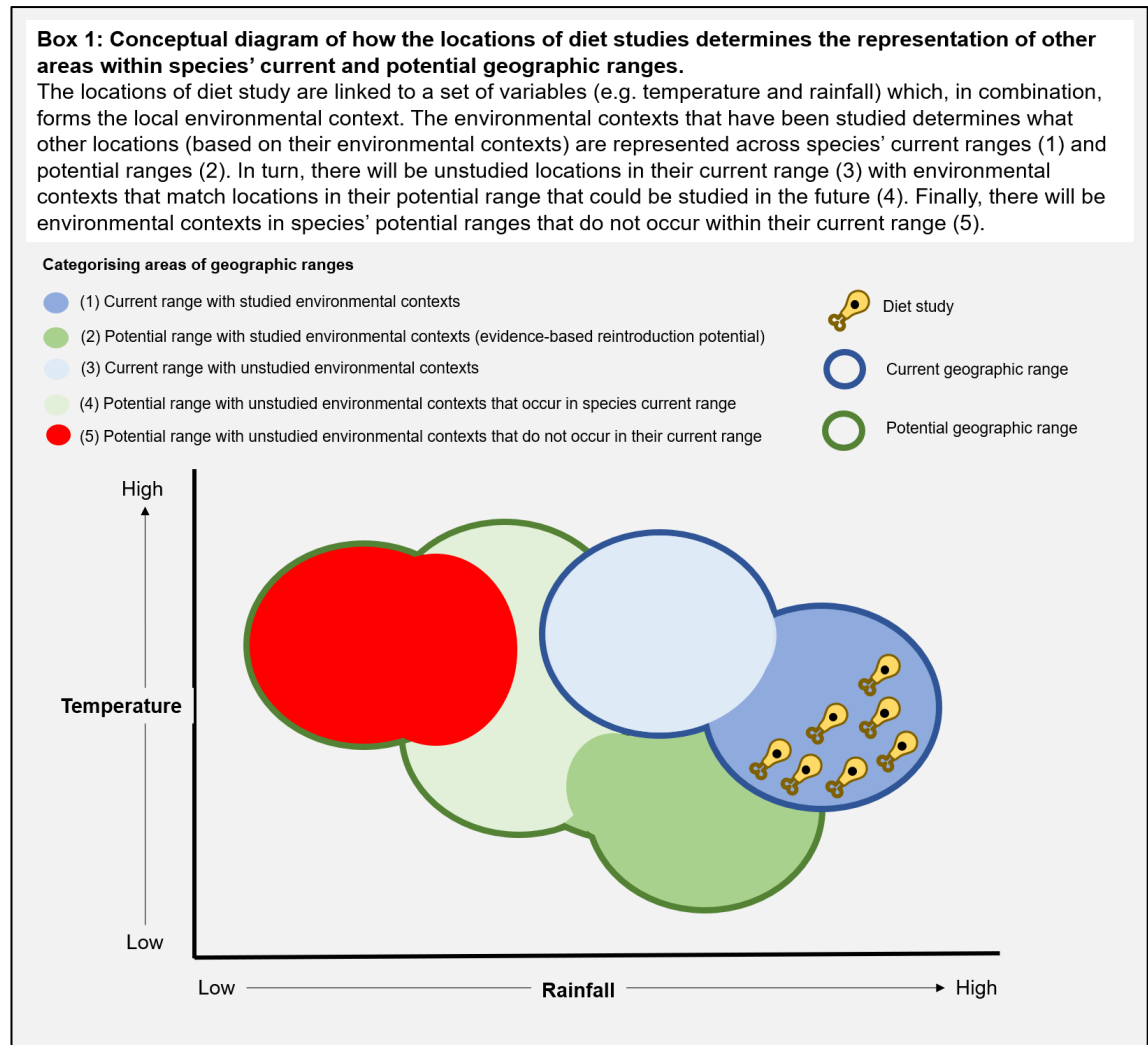
standardized hypervolume construction across species by using a quantile threshold (τ) of 1 and a Silverman bandwidth estimator ($\hat{h}$) (Silverman, 1992) for a global hypervolume that included environmental contexts across all terrestrial areas.

5.3.3 | Identifying studied environmental contexts

We identified the environmental contexts a species' trophic interactions have been studied by identifying areas with a unique study site's centroid coordinates from CarniDIET 1.0 (Middleton *et al.* 2021). We constructed 'studied' hypervolumes for each species by only using the environmental contexts where a species had been studied. For studied hypervolumes, we multiplied the global Silverman bandwidth estimator by two, which, in comparison to the current and potential hypervolumes, added a larger buffer around each studied environmental context within the environmental niche breadth hypervolume. In doing so, we assumed that each diet study represented areas with similar abiotic and biotic conditions that neighbour them within the environmental niche breadth. We then identified the proportion of overlap of species studied hypervolumes with their potential and current environmental niche breadth hypervolumes using the '*get_volume*' function.

5.3.4 | Linking the environmental contexts of diet studies to areas across species' geographic ranges

We first categorised species geographic ranges by whether the areas have environmental contexts that (i) have been studied, (ii) could be studied in their current range but are not, and (iii) cannot be studied within their current geographic ranges. This resulted in five categories between species' current and potential geographic ranges (Box 1): (1) current-studied, (2) potential-studied, (3) current-unstudied, (4) potential-unstudied, and (5) potential-impossible. To do this, we identified areas across species' potential and current geographic ranges with environmental contexts within species' studied hypervolumes using the '*hypervolume_project*' function. This step, and all subsequent analyses, were repeated for environmental contexts described using two and five environmental variables, which respectively reflected increasing resolution from biomes (temperature and rainfall) to ecoregions divided into locations with varying human impacts (plus elevation, mammal species richness, and human influence index).



First, we investigated the difference in geographic scope for evidence-based reintroductions compared to in-situ conservation by calculating the area represented in their potential range relative to the area represented in their current range. Second, we identified whether the geographic distribution of existing knowledge is biased in terms of the environmental contexts represented. To do this, we compared the representation of species' potential geographic ranges from the actual distribution of study locations to a null model of randomly distributed study locations across their current geographic range. We ran 200 simulations of randomly distributed study locations for each species using the same number of studies they have available and identified whether the actual representation occurred outside of the 95% quantiles of simulated geographic range representation.

Linear mixed-effects models (LMMs) were used to investigate the effect of study effort (number of studies) on the difference in representation between actual and random

study distributions. Species names were included as a random effect nested within taxonomic family to consider phylogenetic structure in the data. Hierarchical partitioning was used for model selection by running models with each fixed effect separately and with interactions to identify the simplest model with likelihood ratio tests (X^2). Significance ($p < 0.05$) of fixed effects were evaluated using X^2 tests between models with each fixed effect and a null model, that only included the nested random effect. Pairwise contrasts of the categorical fixed effect (number of variables) was estimated using the ‘*emmeans*’ function in the ‘*emmeans*’ package (Russell *et al.*, 2021).

5.4 | Results

5.4.1 | The representation of species’ geographic ranges by diet studies

When only two environmental variables were considered, we found that species’ diet studies cover a median of 55% and 38% of their current and potential geographic ranges, respectively. When five environmental variables were considered, species’ diet studies cover a median of 13% and 4.5% of their current and potential geographic ranges (Fig. 5.1). On average, we found that 10% and 28% species’ potential ranges (when two and five environmental variables were used, respectively) consisted of environmental contexts not found within their current ranges (Fig. 1), which was greater for species with a greater extent of range loss (Pearson’s correlation: $t = -6.7$, $p < 0.001$, $\rho = -0.59$)

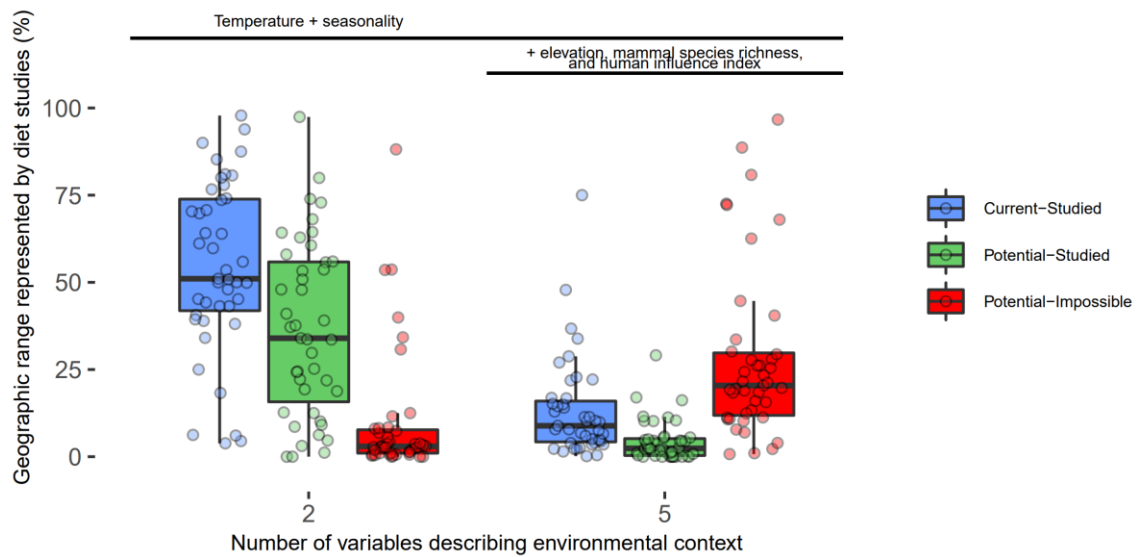


FIGURE 5.1 | Extirpated carnivores’ geographic ranges are only partly represented by existing knowledge of their ecological interactions. The representation (%) of 43 species’ (circles) current (blue) and potential (green) geographic ranges by the environmental contexts of diet studies when using two and five variables to characterize environmental context. The percentage of species’ potential ranges with environmental contexts that do not occur within their current range (red) is also shown. Boxplots indicate the median, and upper and lower quartiles. Whiskers indicate upper and lower values excluding outliers (points) which are values exceeding 1.5 times the interquartile range.

Although extirpated carnivores’ potential geographic ranges were proportionally less represented than their current ranges, this does not necessarily indicate a consistently greater geographic extent of area represented because potential ranges are often larger. Species’ potential ranges were a median of half the size of their current range (lower quartile = a quarter of the size; upper quartile = 3.25 times larger) but could reach up to 142 times larger (red wolf [*Canis rufus*]). We found the represented areas within potential ranges was, on average, 30% that of represented area in current ranges (Fig. 5.2). This indicates opportunities exist for evidence-based predictions of reintroduction outcomes but the geographic scope for evidence-based in-situ conservation typically exceeds this for most species. However, species with the most restricted geographic ranges tended to have >100% additional area in their potential range represented by diet studies compared to their current range, indicating the geographic scope for predicting reintroduction outcomes exceeds that of in-situ conservation efforts (Fig. A5.3).

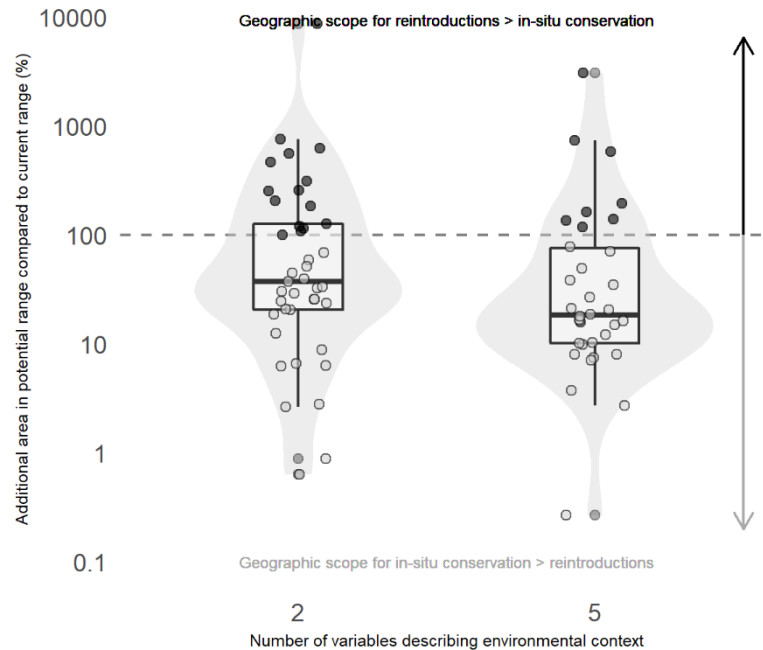


FIGURE 5.2 | The geographic scope for evidence-based predictions of extirpated carnivore reintroductions compared to in-situ conservation. Species with >100% additional area represented by diet studies in their potential range, compared to only in their current range, have a greater geographic scope for reintroductions than for in-situ conservation within their current range (black circles) and typically have the most severely restricted current range (Fig. A5.4). Eight species did not have additional area in their potential geographic range and were excluded here. No significant difference was detected between the two levels of complexity describing environmental context (Wilcoxon rank-sum test; $Z = 1.78$, $p = 0.07$).

5.4.2 | Case-studies

Grey wolves are currently restricted to 81% of their potential geographic range following their extirpation from most of North America and areas in Southern and Western Eurasia. We identified 68 unique diet study sites (Fig. A5.4). The environmental contexts of these sites proportionately represented their current and potential geographic range to similar extents (~19%; Fig. 5.3a). Areas with unstudied environmental contexts typically consisted of areas with combinations of higher temperatures, have lower rainfall seasonality, and at higher elevations (Fig. 5.3b). A total of 19.5% of their potential range consists of environmental contexts impossible to study in their current range, which includes areas with higher temperatures, elevations, human impacts, and species richness. When just two variables (temperature and rainfall seasonality) were used to represent environmental contexts, geographic range representation was much higher across current and potential ranges (~65%) and areas impossible to study reduced to just 0.5% of their potential range (Fig. A5.5a).

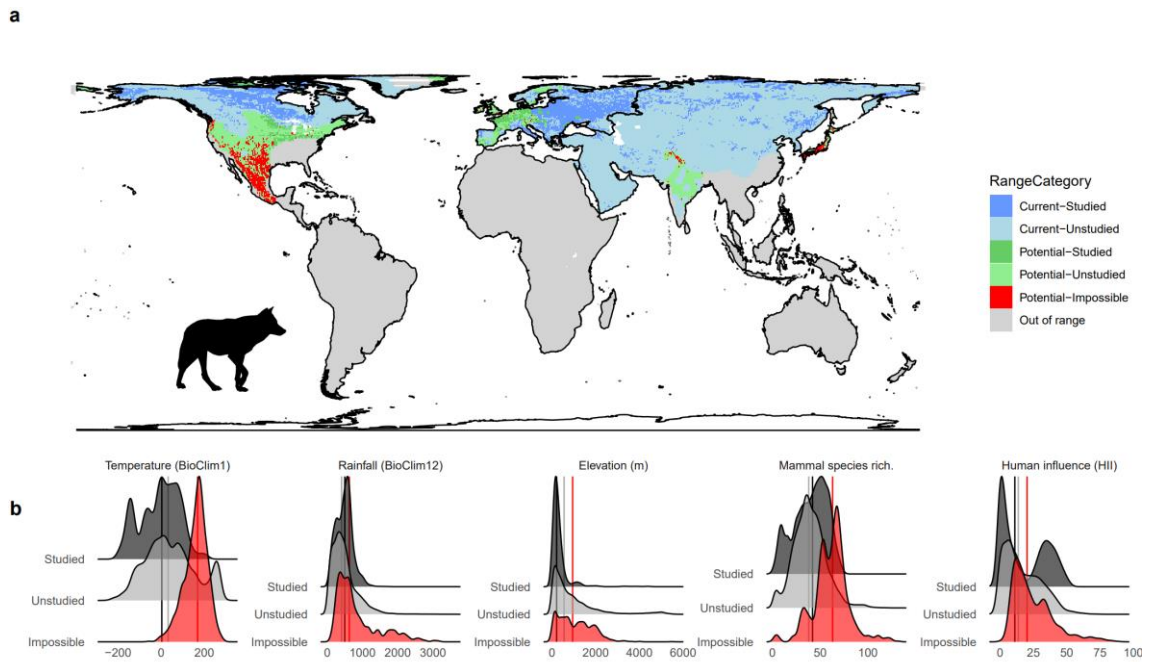


FIGURE 5.3 | Representation of the geographic range of grey wolves by their diet studies. (a) Areas with environmental contexts (combinations of temperature and seasonal rainfall) across the current (blue) and potential (green) geographic ranges that have been studied (darker colours) and could be studied (lighter colours). Red areas indicate environmental contexts in their potential range not found within the current range. (b) The distribution of environmental variables found in studied (black), unstudied (grey), and impossible-to-study environmental contexts (red). Median value of areas are shown with vertical lines.

In contrast, dholes are currently restricted to just 9% of their potential geographic range, which once spanned Eurasia and North America. We identified 12 unique diet study sites for dholes (Fig. A5.3). The environmental contexts of these study sites represented a low proportion of their current (3.5%; Fig. 5.4a) and potential geographic ranges (0.3%). A total of 88% of their potential range consists of environmental contexts that do not occur in their current range, which includes lower temperatures, rainfall seasonality, and species richness. A total of 19.5% of their potential range consists of environmental contexts impossible to study in their current range, which includes areas with higher temperatures, elevations, human impacts, and species richness. When just two variables (temperature and rainfall seasonality) were used to represent environmental contexts, geographic range representation was much higher across current and potential ranges (45% and 24%, respectively) and areas impossible to study reduced to 12% of their potential range (Fig. A5.6a).

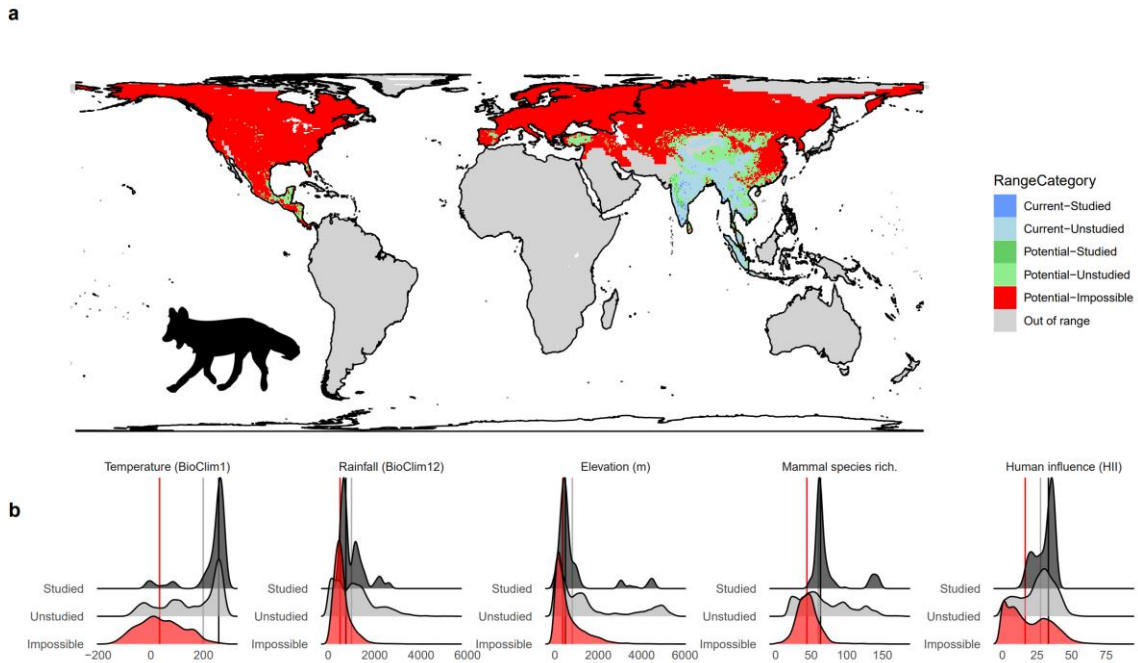


FIGURE 5.4 | Representation of the geographic range of dholes by their diet studies. (a) Areas with environmental contexts (combinations of temperature and seasonal rainfall) across the current (blue) and potential (green) geographic ranges that have been studied (darker colours) and could be studied (lighter colours). Red areas indicate environmental contexts in their potential range not found within the current range. (b) The distribution of environmental variables found in studied (black), unstudied (grey), and impossible-to-study environmental contexts (red). Median value of areas are shown with vertical lines.

5.4.3 | Environmental context bias in diet studies

For 18 and 21 species, when using two and five variables respectively, the combined current and potential geographic ranges were represented by diet studies significantly less than expected from randomly distributed studies (Fig. A5.7). Randomly distributed study locations across the combined geographic ranges would result in its increased representation by, on average, 9% (lower quartile = 2.6%; upper quartile = 18%) and 5% (1%; 10%).

The difference in the representation of species' potential geographic ranges between the actual and random distribution of studies was influenced by study effort and the number of variables describing environmental contexts (LMM: $X^2 = 21.3$, $df = 2$, $p < 0.001$; Fig. 5.5). Species with more diet studies had a greater difference in the representation of their geographic ranges ($X^2 = 12.7$, $p < 0.001$, $df = 1$, $slope = -6.5$; Fig. 5.5) and was lower when using five compared to two variables ($X^2 = 8.6$, $df = 1$, $p = 0.003$; pairs contrast post-hoc: $t_{42} = 2.4$, $p = 0.004$).

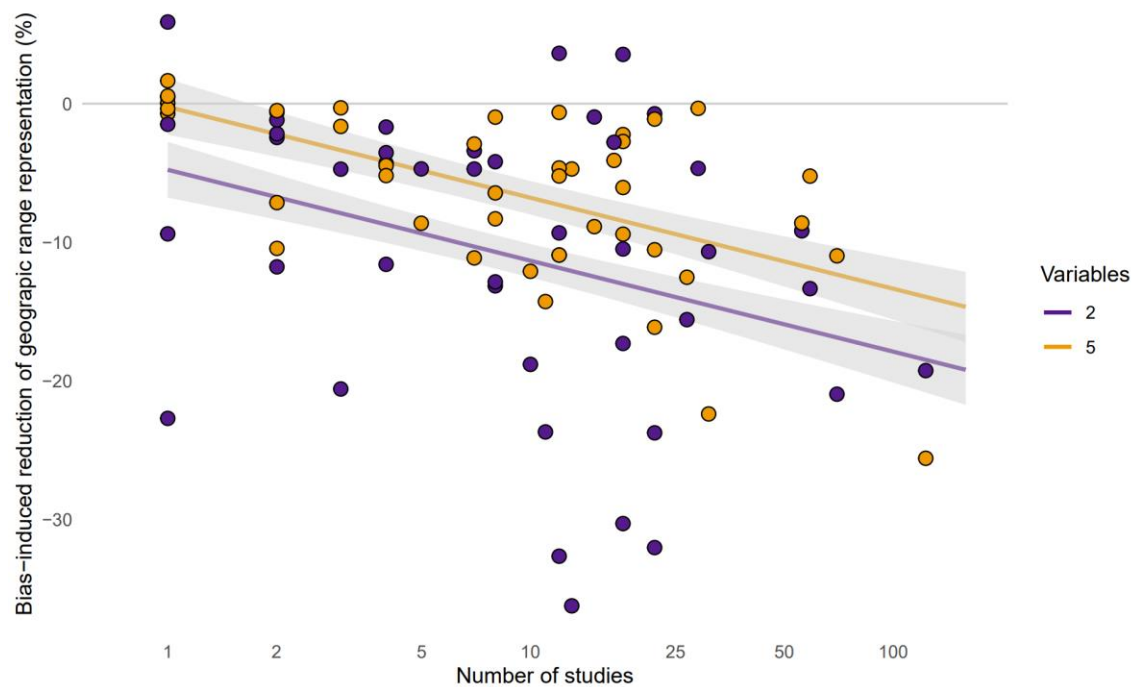


FIGURE 5.5 | Species’ geographic ranges are represented less than expected compared to randomly distributed studies. Species with greater study efforts have an increasingly greater difference in representation than expected from random. Colours correspond to the number of variables describing environmental context. Regression lines indicate predicted LMM values, with ribbons (shaded area) indicating model standard error.

5.5 | Discussion

The potential ecological interactions of extirpated carnivores remain largely unknown across the range of environmental contexts they currently, or have the potential to, occupy. Despite this, we found that widespread opportunities for evidence-based predictions of reintroduction outcomes exist for most extirpated carnivores. However, the geographic scope for these opportunities were consistently lower than expected because research has typically occurred in study sites with similar environments relative to the variety of environments that species occur in. Therefore, future research efforts could prioritize unstudied environmental contexts to increase the geographic scope for evidence-based conservation efforts, including trophic rewilding.

The fact that ecological knowledge is often geographically biased is well known (e.g. Martin *et al.* 2012), although the potential implications of geographic bias in species-specific research has only recently been explored (Mengüllüoğlu *et al.*, 2018; Christie *et al.*, 2020; Britnell *et al.*, 2021; Hughes *et al.*, 2021). In this study, we quantitatively

demonstrate the extent of such geographic bias for extirpated carnivores. Carnivores with larger geographic ranges are typically better studied (Brooke *et al.*, 2014), which may be justified by the wider range of environmental contexts they occupy. Yet, we found research bias for these species was greatest, indicating well-studied species are not necessarily studied across the wider variety of environmental contexts in which they occur. Instead, sites with similar environmental contexts tend to be used to study species diets, which could skew perceptions of species' potential foraging ecologies (Britnell *et al.*, 2021). The implications of such bias were unexplored in this study, but many species of carnivore are known to have varied diets across environmental contexts (e.g. Bojarska & Selva 2012; Díaz-Ruiz *et al.* 2013). The degree to which this occurs among individual carnivore species remains largely unknown, but even large and well-studied carnivores can have variable prey preferences across their range (Mengüllüoğlu *et al.*, 2018). As such, future research prioritization should aim to cover unstudied environmental contexts across species geographic ranges to ensure evidence-based decision making in conservation, including trophic rewilding, becomes more geographically widespread.

Despite geographic bias in research on species interactions, widespread opportunities for evidence-based predictions of trophic rewilding outcomes exist. Understanding the opportunities, and limits, for evidence-based trophic rewilding is timely in the UN's Decade on Ecosystem Restoration as reintroductions would contribute to restoring self-regulating biodiverse ecosystems (Perino *et al.*, 2019; Svenning, 2020). However, the data that are readily available to decision-makers to put this into practice (e.g. Middleton *et al.* 2021) are, typically of wider geographic use for evidence-based species conservation in-situ compared to species reintroductions. Yet, carnivores with severely restricted geographic ranges today, such as Iberian lynx (*Lynx pardinus*) or red wolves (*Canis rufus*), have wider geographic scopes for reintroductions than for in-situ conservation efforts. Crucially, the data used in this study represent a subset of the available data on quantitative ecological interactions which should continue to be digitized and made openly accessible to help inform researchers and decision-makers. Additional sources of knowledge, such as traditional ecological knowledge (Gilchrist, Mallory & Merkel, 2005), could further increase evidence-based decision-making across broader environmental contexts.

Species varied in the extent that diet studies represented their geographic range, which was influenced by geographic range size and study effort, as exemplified with the

dhole and grey wolf. For species restricted to fragments of their potential range today, it is currently not possible to study their interactions in environmental contexts that only occur across their potential geographic ranges, which could limit perceptions of their fundamental ecological niche (Faurby & Araújo, 2018; Monsarrat *et al.*, 2019; Britnell *et al.*, 2021). Restoring these species to their former geographic range would be beneficial for conservation by restoring lost interactions in an ecosystem while contributing to species conservation through their range expansion and potentially revealing unknown aspects of their foraging ecology. Alternatively, species that still occupy relatively high percentages of their potential geographic ranges may have limited representation of their geographic ranges if studies are unevenly distributed across their range, as previously demonstrated with the Eurasian lynx (*Lynx lynx*) (Mengüllüoğlu *et al.*, 2018). As such, the environmental context in which knowledge originated should be recognized on a species-specific basis for conservation applications, including reintroduction and recovery assessments (Akçakaya *et al.*, 2020), and research prioritization (Bezanson & McNamara, 2019).

Every location on Earth has a unique environmental context which we described here using a sample of abiotic and biotic conditions. More, or even fewer, variables and their interactions than we used in this study could influence the ecological interactions that species establish. Understanding these will be a critical next step to identify contextual knowledge gaps across species' geographic ranges. Once identified, predictive modelling could help fill knowledge gaps across environmental contexts without further extensive field studies, although further field studies would likely be necessary (Johnson *et al.* 2020). For carnivore diets, biogeographical patterns have been described (Zhou *et al.*, 2011; Bojarska & Selva, 2012; Díaz-Ruiz *et al.*, 2013), including increased carnivory at higher latitudes (Vulla *et al.*, 2009). Such patterns could be utilized to make predictions across current, and potential, geographic ranges, something previously done for cats (*Felis catus*) in Australia (Woinarski *et al.*, 2017). For under-studied species, data could be pooled amongst species into ecologically realistic functional groups, or taxonomic surrogates used, to boost predictive capability, albeit at the cost of reducing reliability and taxonomic precision which may, or may not, be sufficient for decision-makers (Carbone *et al.*, 1999; Hirt *et al.*, 2020).

Our findings support the growing recognition that unstudied environmental contexts should be prioritized in further data collation and field studies to increase our

understanding of the natural world (Britnell *et al.*, 2021; Christie *et al.*, 2021; Hughes *et al.*, 2021). In doing so for extirpated carnivores, conservationists would increase the geographic scope for both their in-situ conservation and reintroductions, and even reveal previously unknown or unacknowledged aspects of their ecology. In the meantime, generalizing ecological knowledge across different environments, particularly environments yet to be studied, should be done cautiously, whether this be as evidence for species ecological effects, including introduced species, or for predicting the outcomes of species introductions. In the UN's Decade on Ecosystem Restoration, facilitating recolonizations and reintroductions of extirpated carnivores, where possible, to areas of their former range will be fundamental to restore ecosystem trophic complexity. Overall, we show that existing data on extirpated carnivore ecologies is sufficient to begin facilitating widespread evidence-based predictions of their reintroduction outcomes.

CHAPTER 6 | Recently established predators rewire Australia's mammalian food webs

“Maybe if we started looking at what's the same instead of what's different...well, who knows.”

Meowth

6.1 | Abstract

Since the Late Pleistocene (LP; ~130,000 – 11,700 ypb), humans have driven species' extinctions and colonisations, which have modified ecosystem functioning worldwide. Species that recently colonized ecosystems can contribute to extinctions but can also enhance ecosystem complexity by rewiring the structure of simplified interaction networks. For mainland Australia, we assessed how the structures of current-day mammalian predator communities and food webs, which include the recently established dingo, red fox, and cat, as well as several herbivores, compare to those from the LP, prior to human-driven extinctions. We compiled functional traits that influence predator-prey dynamics for all medium-large predators (>1 kg) that have occurred in Australia since the LP and estimated all potential pairwise interactions between co-occurring predator and prey species using the best available evidence for each predator's diet. While recently established predators are functionally distinct because of their smaller body masses, we found that they rewire the structure of food webs that were simplified following LP extinctions. However, recently established predators are more reliant on smaller prey species than extinct predators. A key ecological role that can influence ecological dynamics has also been restored, wherein protected dingo packs today show resemblance to the role of marsupial lions. Dingo persecution, however, decreases the resemblance of current-day food web structures to those existing before LP extinctions, and increases the influence of mesopredators in food webs. In scenarios without predator persecution, however, dingoes, foxes and cats rewire food web structures and restore ecosystem trophic complexity to mainland Australia.

6.2 | Introduction

Prehistoric and historic human-induced extinctions of large animals have caused widespread loss of top-down interactions and simplification of ecosystem trophic complexity (Estes *et al.*, 2011). Ecosystems have also gained interactions through species that have recently established novel populations, often through human-assisted colonization (Wardle *et al.*, 2011). The conservation community typically views these species as drivers of extinction (Bellard, Cassey & Blackburn, 2016), particularly mammalian predators (Doherty *et al.*, 2016), rather than contributing to biodiversity (Wallach *et al.*, 2020). Yet, recently established species can act as counter currents to extinction by increasing species richness (Lundgren *et al.*, 2018; Wallach *et al.*, 2020) and restoring ecological functions (Lundgren *et al.*, 2020). However, it remains unknown whether the interactions from recently established mammalian predators rewire food webs so that their structures resemble those before human-induced extinctions (Pires, 2017).

Australia's predator and broader mammal community has been modified by extinctions and colonisations since modern human arrival ~65,000 years before present (ybp) (Clarkson *et al.*, 2017). Throughout the Late Pleistocene (LP; ~130,000 – 11,700 ybp), extinctions primarily affected larger species, including the marsupial lion (*Thylacoleo carnifex*), Australia's apex mammalian predator. By the mid-Holocene (~3000 ybp), thylacines (*Thylacinus cynocephalus*) and Tasmanian devils (*Sarcophilus harrisii*) had gone extinct on the mainland, leaving the tiger quoll (*Dasyurus maculatus*, 1-5 kg) as the largest marsupial mainland predator. Excluding recently established predators, Australia currently has the most depauperate continental predator community (Middleton *et al.*, 2020).

However, three predators recently established populations in Australia during the Holocene. Dingoes (*Canis dingo*) established $\geq 5,000$ ybp following dispersal across a land bridge from Papua New Guinea, potentially with human assistance (Cairns & Wilton, 2016). A major shift occurred following European human arrival ~250 ybp: red foxes (*Vulpes vulpes*) and cats (*Felis catus*) established thriving populations and the geographic range of tiger quolls was reduced. Dingoes also became, and continue to be, widely persecuted to reduce perceived threats to livestock despite being a protected species. A wave of extinctions ensued, primarily affecting small mammals (35-5,500 g),

the preferred prey of foxes and cats (Cardillo & Bromham, 2001). Australian foxes and cats are thus considered the driver of recent extinctions and population declines, despite widespread habitat degradation following European arrival (Woinarski *et al.*, 2015).

The lack of coevolution with recently established predators is hypothesized to cause adverse effects to Australia's small mammals (Carthey & Blumstein, 2018). As marsupial and placental predators are separated by millions of years of evolution, they are argued to diverge in traits that influence prey consumption, such as body mass and hunting modes (Short, Kinnear & Robley, 2002). Despite this, dingoes and thylacines are typically considered ecological equivalents, although thylacines had a smaller average body mass (~16.7 kg) than previously estimated (Rovinsky *et al.*, 2020) and likely small- to mid-sized prey specialists (Rovinsky, Evans & Adams, 2021). Conversely, socially-stable dingo packs can hunt large prey, including recently established megafauna, such as donkeys (*Equus asinus*) (Wallach *et al.*, 2009), horses (*E. ferus*) (Dr Arian Wallach, personal observation), water buffalo (*Bubalus bubalis*), and sambar deer (*Rusa unicolor*) (Forsyth *et al.*, 2018b).

While predator traits influence their ability to hunt specific prey species, the effects of predator-prey interactions on prey populations are also influenced by interactions among predators (Prugh & Sivy, 2020). Top-down interactions from apex predators have cascading ecological effects that can influence the identity and magnitude of interactions between other predators and their prey. In Australia, dingoes can influence population densities and behaviours of cats and foxes (Brook, Johnson & Ritchie, 2012; Leo, Reading & Letnic, 2015) and are argued to drive top-down forces in Australian food webs (Wallach *et al.*, 2017a). However, widespread dingo persecution fractures dingo packs and reduces their ability to hunt large prey and influence mesopredator populations, leading to stronger predation pressures on small prey (Johnson *et al.*, 2007; Wallach *et al.*, 2009, 2010). High and sustained persecution pressures can even cause dingoes to become functionally extinct (Säterberg, Sellman & Ebenman, 2013), which is widespread south of the dingo barrier fence, which was designed to eradicate dingoes from south-eastern Australia.

Here, we analysed how mammalian extinctions and colonisations have influenced the structures of Australia's mammalian predator communities and food webs through time. We constructed species lists for four time periods that reflect modifications to

Australia's predator community: earliest-LP (~130,000 – 115,000 ybp), early-Holocene (~11,700 ybp), mid-Holocene (~3,000 ybp), and current-day. We focused on whether dingoes, foxes, and cats can collectively rewire the structure of current-day food webs to resemble LP food web structures before human-induced extinctions. For comparability across time periods, food webs were represented using metawebs which include all potential predation links between co-occurring predators and prey, rather than observed interactions which cannot be obtained for extinct communities. We investigated three aspects of ecological change, including (i) the functional trait composition of the predator community at the continental-level, (ii) food web structures at the biome-level, and (iii) ecological roles of predators within food webs. For each, we investigated the implications of dingoes becoming functionally extinct in the current-day, following severe persecution, compared to a scenario in which their populations are protected.

6.3 | Methods

6.3.1 | Species lists reflecting modifications to Australian mammal communities

We constructed mammal species lists for mainland Australia reflecting: (i) before Late Pleistocene (LP) extinctions (~130,000 – 115,000 ybp); (ii) after LP extinctions but before dingo arrival (~11,700 ybp; 'early Holocene'); (iii) after dingo arrival and mainland Tasmanian devil and thylacine extinction (~3,000 ybp; 'mid-Holocene'); (iv) current-day after fox and cat establishment, and quoll range reduction. We used 'present-natural' species' ranges to identify LP mammals and differentiated those that became extinct in the LP or after European arrival using Faurby *et al.* (2018). Present-natural ranges are suitable proxies for mammal ranges during the last interglacial as they are estimates of mammal ranges in the current interglacial for a counterfactual scenario where species ranges are not restricted by humans. We used 'current' maps from Faurby *et al.* (2018) to identify mammals remaining today. Maps derived from Lundgren *et al.* (2020) were used to identify Holocene-established mammals.

For each time period, we selected hypercarnivorous ($\geq 70\%$ vertebrate meat), medium-large mammals (>1 kg) as predators (traits from Faurby *et al.* (2018)). We identified five marsupial predators: marsupial lions (*Thylacoleo carnifex*), thylacines (*Thylacinus cynocephalus*), tiger quolls (*Dasyurus maculatus*) and Tasmanian devils (*Sarcophilus harrisi*). A giant rat-kangaroo (*Propleopus oscillans*) may have also been

hypercarnivorous, but we excluded it because little knowledge of its ecology exists. We identified three Holocene-established predators: dingoes (*Canis dingo*), red foxes (*Vulpes vulpes*), and cats (*Felis catus*).

6.3.2 | Australian predator community structures

We collected seven functional traits for each predator, including average body mass, maximum prey size, hunting modes (pursuit/pounce-pursuit/ambush), locomotion (cursorial/scansorial/generalised), hunting group size, bite force, and fecundity ([litter size × litters per year] / reproductive group size). Traits were collected separately for protected and persecuted dingoes, and for social and solitary marsupial lions to reflect uncertainty in sociality. We calculated pairwise Gower's distances between predator trait compositions because, although traits were weighted equally, categorical traits (e.g. locomotion) were individual binary traits weighted by a proportion of the number of categories (e.g. cursorial/scansorial/generalized each weighted by 1/3) (Lundgren *et al.*, 2020). A principal coordinate analysis was performed with a Cailliez correction to correct for negative eigenvalues (Laliberté *et al.*, 2014). We used the 'envfit' function in the R package 'vegan' (Oksanen *et al.*, 2013) to identify traits structuring the first two axes (76% variance; Table S3) using squared correlation coefficients (r^2).

Two functional diversity metrics were calculated for each time period's predator community using the 'FD' package (Laliberté *et al.*, 2014). Functional richness is the minimum convex hull volume of all species and describes trait composition diversity, varying from 1 (all predators present) to 0 (< 3 predators) (Villéger *et al.*, 2008). Functional dispersion is the average distance of predators from the community centroids and describes average species dissimilarity (Laliberte & Legendre, 2010).

6.3.3 Constructing food webs for Australian biomes

We identified the best evidence for each predator's diet to estimate interactions with prey. For extant predators, we extracted quantitative diet studies in Australia from Middleton *et al.* (2021), including red foxes ($n = 29$), tiger quolls ($n = 9$), and Tasmanian devils ($n = 3$). Dingo ($n = 33$) and cat ($n = 14$) diet studies were not available and collated separately (Fig. A6.1). For thylacines, we used anecdotal observations of prey interactions and suggested prey from functional morphology studies (justifications in the Appendix section 5.1). For marsupial lions, we extracted diet studies from Middleton *et al.* (2021) for tigers, (*Panthera tigris*; $n = 26$), lions (*Panthera leo*; $n = 21$), and jaguars (*Panthera*

onca; $n = 17$) as potential diet proxies (Fig. A6.2a). The genus *Sthenurus* (72-173 kg) were likely common marsupial lion prey (Case, 1985), so we considered extant felid diets as suitable proxies if they included *Sthenurus* mass range as common prey.

Diet studies reporting frequency of occurrence of prey were used, reflecting predator-prey interaction frequencies. Prey were defined as ‘common’ when in $\geq 20\%$ of diets, ‘occasional’ in $\geq 5\%$ and $< 20\%$, and ‘rare’ in $< 5\%$. If prey were not described at the species-level, the species richness of the prey taxonomic group at the study site was identified. Frequency of occurrence was divided by the species richness and the median body mass used. For thylacines, we assigned common prey from 1-5 kg, occasional prey from 1-30 kg, and rare prey up to 46 kg (Wroe *et al.*, 2007). The common prey of tigers and lions were comparable and included *Sthenurus* body mass range (Fig. A6.2b). For this analyses, we used lion diets as they included a lower prey body mass limit that large predators could handle and consume (Gravel *et al.*, 2013). Maximum prey body mass of persecuted, and functionally extinct, dingoes was restricted to the body mass of red kangaroos as this was the largest prey species observed to be successfully hunted by a single dingo (46 kg) (Thomson, 1992).

We identified all potential interactions between co-occurring predators and prey for each biome and time period. We identified species biome occurrence (Olson *et al.*, 2006), whereby overlap in species ranges with a biome indicated biome membership. Present-natural ranges are compatible with current-day biome distributions and likely reflect biomes that extinct species would have been associated with in the LP. For the LP, early- and mid-Holocene species lists, we used present-natural maps, assuming extant species’ range contractions occurred post-European establishment. Current-day ranges were used for the current-day species lists. Each prey species had its dietary importance assigned to each predator, depending on the predator’s common (strength = 3), occasional (strength = 2) and rare (strength = 1) prey thresholds. These were interpreted as potential interaction strengths, although realized interaction strengths are context-dependent.

We assessed all possible intraguild interactions between predators (Table A6.2). We removed intraspecific interactions and those with a larger predator. All remaining interactions were given the strongest potential interaction strength to reflect the influence of intraguild interactions on the effects of predators on prey. Intraguild interactions were added from foxes to tiger quolls. We added weak competitive interactions between tiger

quolls and cats in both directions and for Tasmanian devils and tiger quolls in a single direction. For persecuted, and functionally extinct, dingoes we removed interactions with smaller predators to reflect their negligible top-down ecological effects in this persecuted context (Wallach et al. 2009).

Each adjacency matrix of predator-prey interactions were converted into food webs as a directed unipartite network with the ‘*igraph*’ package (Csardi, 2015). We used potential interaction strengths between species as weightings in food webs.

6.3.4 | Food web structures and the ecological roles of predators

We identified changes in the number and strength of interactions between predators and five categories of prey body mass (<0.1 kg, 0.1-1 kg, 1-10 kg, 10-44 kg, and >44 kg) from the LP to current-day. The >44 kg cut off was used to represent megafauna (Saltr   et al., 2019) and the disproportionate ecological effects they have in structuring ecosystems (Enquist et al., 2020). For each category, we identified the number of interactions lost and gained for: (i) native prey following predator extinctions and recent establishments, (ii) the remaining native predator following prey extinctions and recent establishments, and (iii) from extinct predators and prey and recently established predators and prey.

We investigated food web structures for each time period and biome by calculating seven metrics using the ‘*omnivor*’ (Violet & Gravel, 2019) and ‘*NetIndices*’ (Soetaert, Kipyegon Kones & van Oevelen, 2015) packages, including: (i) number of species, (ii) number of interactions, (iii) average species interaction density, (iv) connectance, (v) compartmentalisation, (vi) nestedness, (vii) and number of intermediate species. We also calculated mean body mass of species in food webs. Ecological roles of predators in food webs were calculated using four centrality metrics: (i) degree, (ii) betweenness, (iii) closeness, and (iv) eigenvector using the ‘*igraph*’ package. We also calculated mean body mass of prey. Descriptions of all metrics are in the Appendix. For the current-day time period, we compared the structure of food webs with and without dingo persecution, whereby persecuted dingoes were limited to interacting with prey $\leq$ 46kg and without interactions with smaller predators.

We identified changes to food web structures across the four time periods and the ecological roles of predators in the LP and current-day food webs using principal component analyses (PCA) with the ‘*prcomp*’ function. Individual observations in PCAs included biome-level food web structures and ecological roles of each predator’s role

within food webs for each time period analyzed, respectively. As above, for the current-day time period, we compared the roles of predators in food webs with and without dingo persecution.

6.4 | Results

For medium-large predators (>1 kg and $\geq 70\%$ vertebrate meat consumption), we compiled seven traits that influence predator-prey dynamics (Appendix section 5.1 for justification). For each time period we constructed predator functional trait spaces, by performing principal coordinates analyses on the pairwise-dissimilarities of predator trait compositions. To assess changes to the predator community structure, we calculated two functional diversity measures.

Doing so, we found that LP extinction of the marsupial lion caused an 85% decline in predator functional richness and 50% in functional dispersion, functional metrics that describe trait diversity and the average dissimilarity between species, respectively (Fig. 6.1B & C). Dingo establishment and extinction of thylacines and Tasmanian devils resulted in only two predator species remaining, causing functional richness to decline to zero (Fig 6.1B) but increased functional dispersion by 33%, relative to the LP (Fig 6.1C). Fox and cat establishment, alongside dingoes, in current-day communities increased functional diversity but is influenced by whether dingoes are protected or persecuted. Where protected, functional richness is 71% greater than the LP, versus 11% where persecuted. Likewise, functional dispersion is 16% greater than the LP where protected and 2% greater where persecuted. Recently established predators occupy distinct regions of functional space because of smaller body masses and maximum prey sizes compared to LP predators, and higher fecundities, but also because dingoes are functionally distinct as cursorial pack-hunters allowing them to hunt large prey relative to their body mass. Similar functional dispersion between the LP and current-day indicates comparable predator community structures, both consisting of an apex predator and three small-prey specialists.

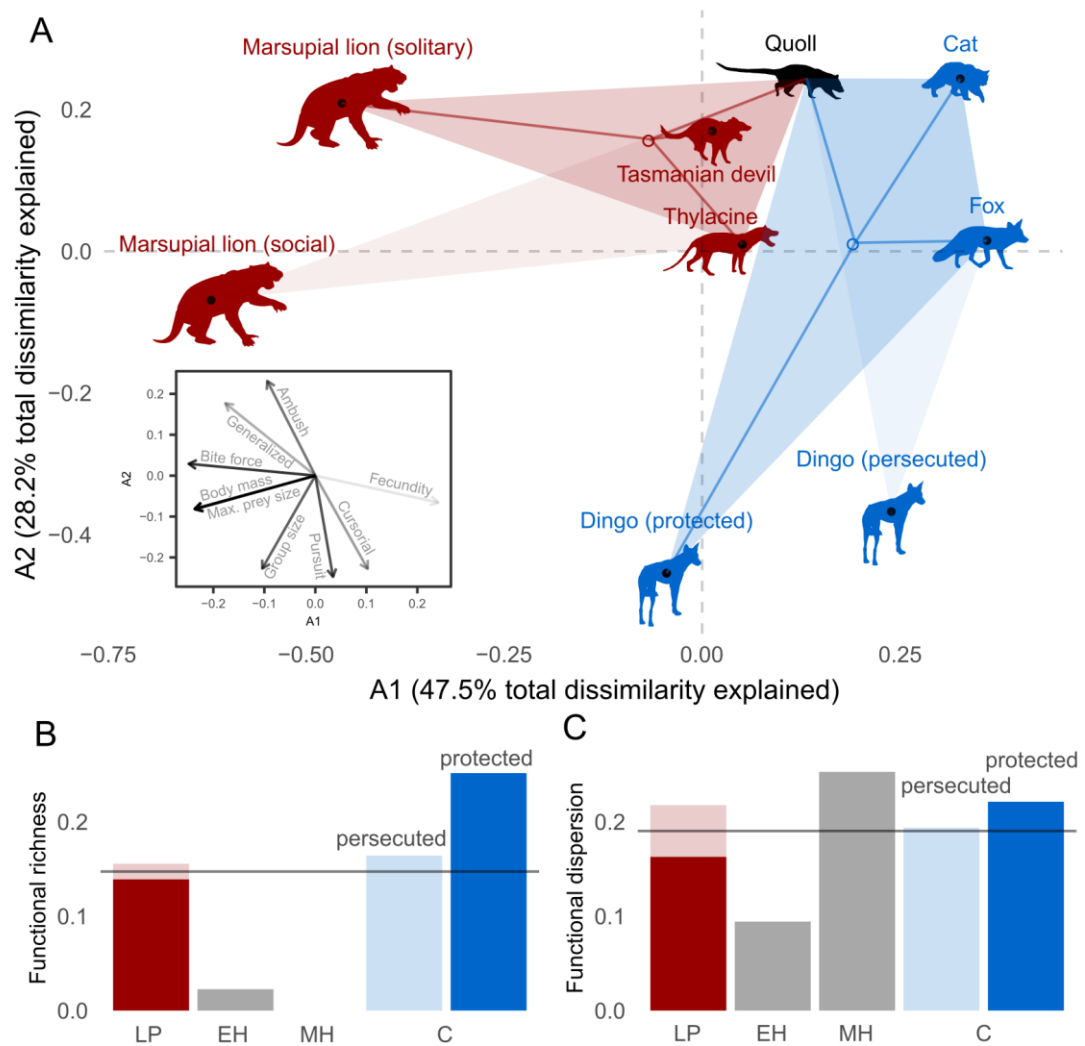


FIGURE 6.1 | Shifts in Australian predator functional space following predator extinctions and recent establishments. (A) Predator functional trait space for mammalian predators that have occurred on mainland Australia in the past ~130,000 years (Table A6.1), including extinct (red), extant-native (black), and recently established (blue) predators. Distances between species reflect pair-wise dissimilarity in trait compositions. Convex hulls are shown for the Late Pleistocene community (red polygon) with solitary and social (more transparent) marsupial lions, and for the current-day community (blue polygon) with protected and persecuted (more transparent) dingoes. Open circles indicate community centroids and lines show species distances from centroids. Arrows (inset) show traits structuring functional space (darker indicates a higher r^2). (B) Functional richness and (C) functional dispersion for each time period (LP = Late Pleistocene, EH = early-Holocene, MH = mid-Holocene, C = current-day). Horizontal lines indicate midpoints of LP functional diversity measures for comparison to other time periods.

Despite differences in body mass and maximum prey body mass between extinct and recently established predators, overlap occurs in their potential (extinct and recently established) mammalian prey (Fig. 6.2). We estimated common, occasional, and rare prey body mass ranges for each predator using the best evidence available for their diets and identified all potential interactions between co-occurring predator and prey species for each time period. The interactions that prey gained from recently established predators

numerically replace those that native (i.e. extant and occurred in Australia during the LP) prey lost with extinct predators, although the extent of those replaced varies between prey body mass categories (Table A6.2). For large (>10 kg) native prey, 50% of lost interactions were replaced by recently established predators, while almost all lost interactions have been replaced for small (<1 kg) native prey, but an 8% increase in interactions for prey <0.1 kg because recently established predators have smaller prey body mass ranges. Recently established predators collectively rely on smaller-bodied prey species more than extinct predators and thus can establish stronger interactions.

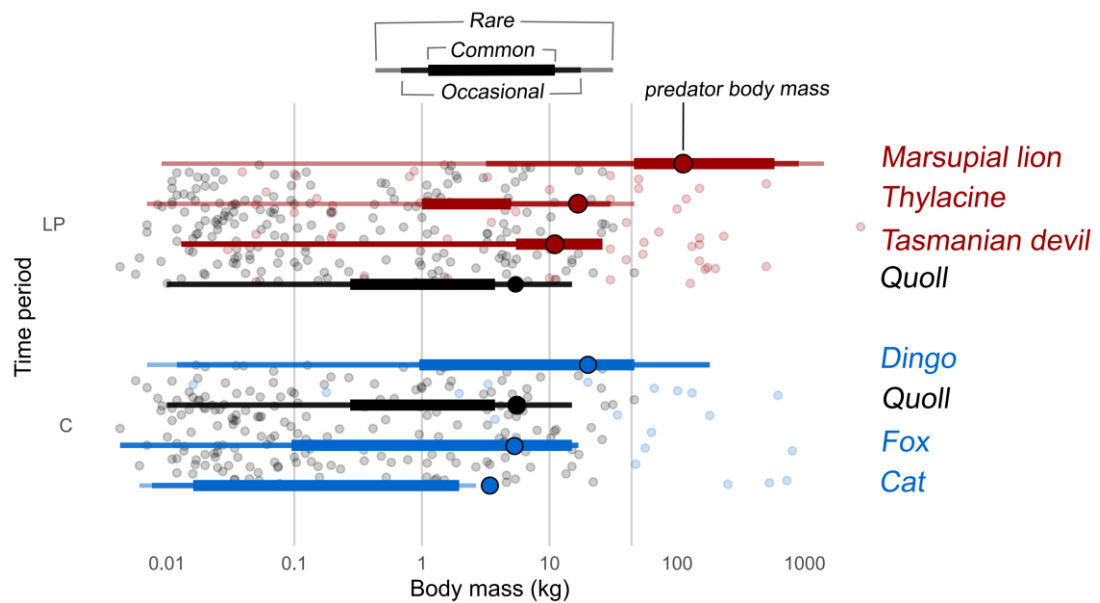


FIGURE 6.2 | Potential prey body mass ranges of Australian mammalian predators. Body masses are shown for extinct (red), extant-native (black), and recently established (blue) predators (larger circles) and prey species (smaller circles) that occurred on mainland Australia in the Late Pleistocene (LP) and the current-day (C). Prey ranges are for solitary marsupial lions, and protected dingoes. Body mass ranges for commonly, occasionally, and rarely consumed prey species for each predator are indicated by varying line thickness. Vertical grey lines indicate break points for prey body mass categories.

We then investigated how predator extinctions and recent establishments have influenced Australian food web structures. Prey had a dietary importance assigned for each predator, depending on the predator's body mass range of common, occasional, and rare prey (scored 3, 2, and 1 respectively). We also assessed intraguild interactions between predators which shape other predator's ecological effects (Table A6.3). To identify potentially interacting predator and prey species we conducted this analysis at the biome-level, though report the continent-wide average (see Fig. A6.3 for biome-level

results). We performed two principal components analyses (PCA), first describing food web structures and second describing species' ecological roles within food webs.

We found that current-day food web structures resemble aspects of LP food web structures (Fig. 6.3A). Extinctions simplified food webs by reducing the number and average body mass of predator and prey species, number of interactions per prey species, and number of interactions between predators. However, recently established predators and prey partly restore the average body mass of species in food webs, number of interactions, and number of interactions per prey species. However, connectance and the number of interactions between predators are higher in the current-day, because bi-directional links exist between predators of comparable body masses, compared to LP food webs.

Dingo persecution changes current-day food web structures and reduces their resemblance to LP food webs (Fig. 6.3D & E). Where persecuted, predation links with megafauna are lost because the capacity for dingoes to hunt cooperatively and handle large prey is diminished (Fig. 6.3D), leading to fewer interactions and reduced average body mass of prey species. Connectance and interaction density increase as the remaining smaller prey species in food webs mostly interact with all predators. The number of predators susceptible to predation also declines as top-down interactions from dingoes are diminished.

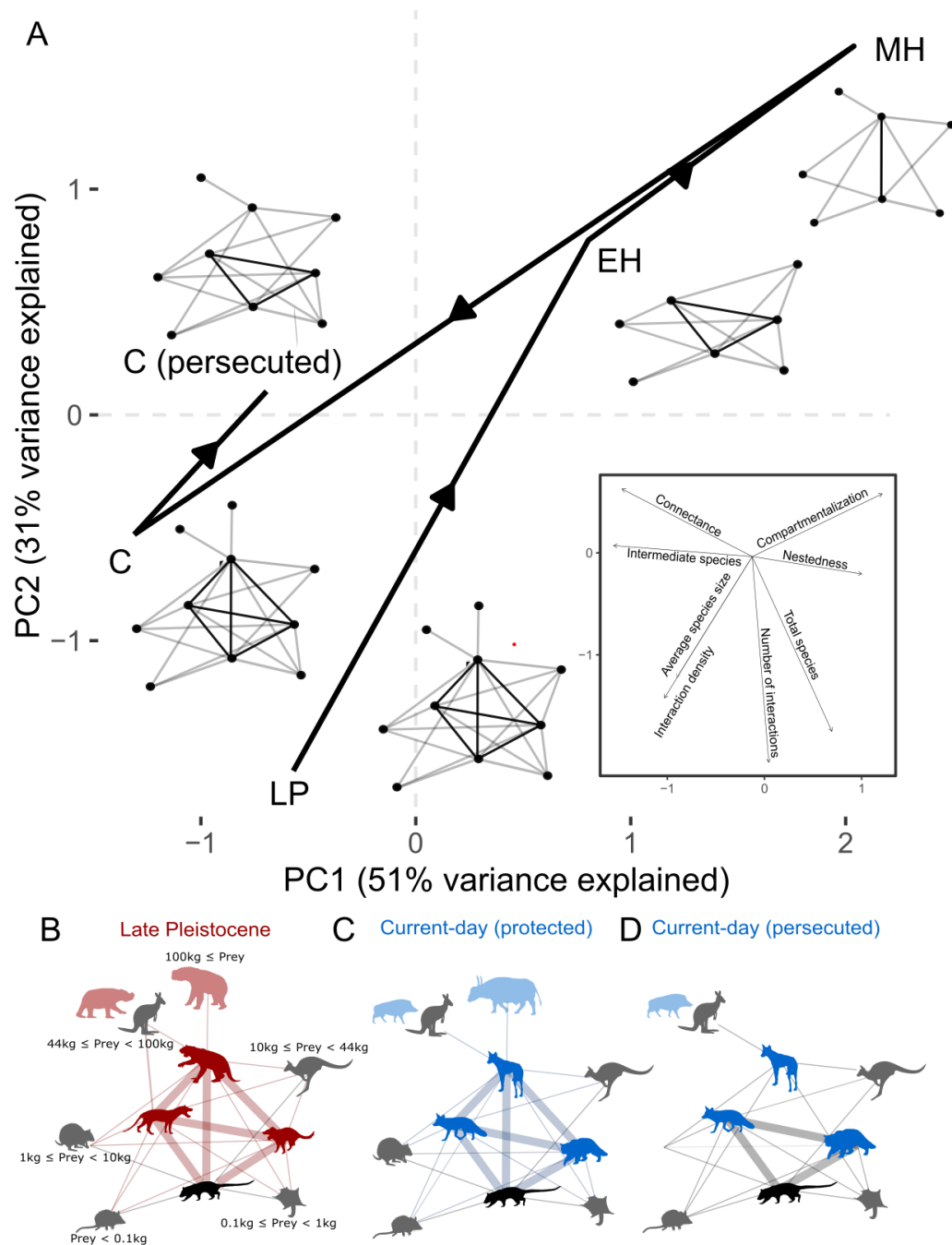


FIGURE 6.3 | Rewiring of Australian food web structures. (A) Average trajectory of change to food web structures across time periods (LP = Late Pleistocene, EH = early-Holocene, MH = mid-Holocene, C = current-day), and following dingo persecution (biome-level points, Fig. A6.3; metrics changes, Fig. A6.4). The first two principal components explained 82% variance. Inset networks are simplified food webs with links between predators and prey categories (lighter lines), and between predators (darker lines). Inset square shows PCA loadings with eight network structure metrics (Table A6.4). Food webs in (a) are shown with detail on predator and prey body mass categories for the community before LP extinctions (B), current-day with persecuted dingoes (C), and current-day with protected dingoes (D). Prey size category labels in (B) are comparable in (C) and (D). Examples of extinct prey (lighter red) and recently established prey (lighter blue) representative are also shown.

Within their respective food webs, the ecological roles of certain extinct and recently established predators align (Fig. 6.4; Fig. A6.5). Protected dingoes closely align with marsupial lions as both consume prey with high average body mass and centrality (i.e. influence in food web). The ecological roles of foxes and thylacines also align, due to comparable average body mass and centrality. Predators of smaller prey occur in a larger cluster overall but those that recently established have higher centralities than those in LP food webs. Dingo persecution, however, modifies the ecological roles of predators in current-day food webs by reducing the influence of dingoes in food webs and increasing that of smaller predators.

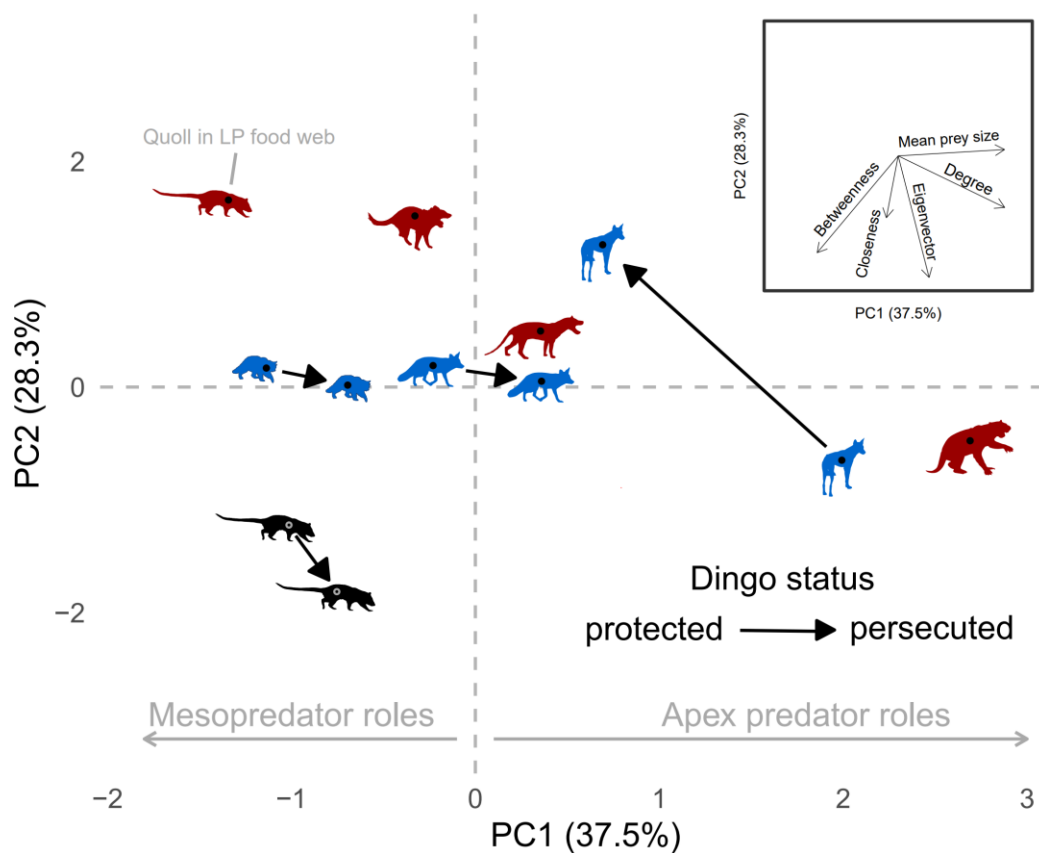


FIGURE 6.4 | Ecological roles of predators in Australian LP and current-day food webs. Positions of extinct (red), extant-native (black), and recently established (blue) predators indicate average ecological role across biome-level food webs (biome-level ecological roles, Fig. A6.5; changes in metrics, Fig A6.6). Arrows show transitions of ecological roles of predators in current-day food webs with protected dingoes to those with persecuted dingoes. The ecological role of quolls in LP food webs is shown in red. Loadings (inset and Table A6.5) are indicated by arrows.

6.5 | Discussion

Broadening our conception of ecological change to encompass prehistoric extinctions reveals that Australia's rewired mammalian food webs have structures that resemble

those before human-induced extinctions. The smaller body masses of recently established predators have created functional differences, although ecological context will influence the outcome of such differences, including whether dingoes are persecuted or not.

Current and LP food webs both possess an apex predator capable of hunting large prey, alongside several small prey specialists. The top-down pressures from dingoes likely mirrors those from marsupial lions in LP ecosystems, echoing research demonstrating that dingoes benefit native mammals by influencing mesopredator populations and behaviours (Johnson *et al.*, 2007). While marsupial lions hunted now-extinct megafauna, recently introduced megafauna could be regulated, at least indirectly, by socially-stable dingo packs if protected (Wallach *et al.*, 2009; Forsyth *et al.*, 2018b). Red foxes also align in their ecological role with thylacines through overlapping prey body mass ranges and the ability to establish top-down interactions with smaller predators. Recent work corroborates this, after showing thylacines were morphologically, and likely ecologically, comparable to small-prey specialized canids (Rovinsky *et al.*, 2020, 2021), although with the capacity to hunt larger prey than foxes can (Wroe *et al.*, 2007).

The capacity for dingoes to assume the ecological role of apex predator is, however, limited by persecution. In food webs with functionally extinct dingo populations, where persecution is severe, mesopredator and large herbivore populations are released from top-down pressures (Wallach *et al.*, 2009, 2017a; Brook *et al.*, 2012). The loss of dingoes as functional apex predators reduces the resemblance of current-day food web structures to those of the LP. Under this scenario, the influence of cats and foxes in food webs increases, as in Wallach *et al.* (2017a); and recently established megafauna become free from predation.

Compared to the LP, recently established predators also add new ecological functions and characteristics to Australian food web structures. Such additions are largely because of their smaller body masses and their potentially greater reliance upon smaller prey compared to their extinct predator counterparts. As small prey today have a higher number of interactions from all predators, and fewer megafauna with a single predator, food webs in the current-day are more highly connected than LP food webs, as previously shown for plant-frugivore networks (Fricke & Svenning, 2020). Therefore, compared to the LP, changes in abundances or extinctions of species will more likely influence other

co-occurring species today, which often occurs where dingoes are persecuted (Johnson *et al.*, 2007). Further, the ecological traits of cats, including wide habitat breadth, could facilitate higher population densities in modified landscapes without dingoes, where cats could create greater predation risks to prey than tiger quolls (Hamer *et al.*, 2021). Yet, the hunting modes of recently established predators may not be as novel as previously suggested (Short *et al.*, 2002). Pounce-pursuit hunting by foxes is potentially not too dissimilar to the generalized ambush or pounce modes suggested for thylacines (Janis & Figueirido, 2014), and cats and quolls also share similar hunting modes (Pellis & Nelson, 1984).

The effects of recently established predators in current-day food webs, as for any predator, will be influenced by ecological context (Wallach *et al.*, 2015b). The high predation pressure that small animals can face from foxes and cats is interconnected with long-term, and widespread, dingo persecution and habitat degradation (Brook *et al.*, 2012; Woinarski *et al.*, 2015). Where ecological context causes predation pressure to be greater than the past, long-term ecological and evolutionary dynamics could be modified for Australian prey species (Faurby & Svenning, 2016), but continued landscape alterations by humans could modify these further (Smith & Bernatchez, 2008). As such, maintaining intact predator assemblages by protecting dingoes will be fundamental to safeguard small animals of conservation concern, alongside stemming ongoing habitat loss.

Mammalian predator-prey food webs today share striking similarities to those of the past, but important uncertainty remains. Reptiles up to seven metres long also hunted mammals before Late Pleistocene extinctions and may have contributed significantly to community dynamics (Wroe, 2002). However, reptilian predators are not thought to be ecological analogues of apex mammalian predators because of their lower per capita metabolic rate requiring a less frequent and less active hunting strategy (Ponds *et al.*, 2020). Therefore, only including mammalian predators in our analyses, which have comparably higher metabolic rates and more active and frequent hunting strategies, likely captures crucial aspects of past and contemporary Australian food webs. Uncertainty also exists regarding the ecology of extinct predators, with largely anecdotal knowledge for the diets of thylacines being limited to Tasmania, whose thylacines tended to be larger-bodied than their mainland relatives (Letnic, Fillios & Crowther, 2012a). Further, the common prey of marsupial lions were thought to be the extinct short-faced kangaroo (sthenurines; Case 1985), with *Sthenurus stirlingi* being the largest species at ~170 kg.

Therefore, the data used in this study could overestimate effects of marsupial lions on prey >200 kg in the past. The full functional capacity for socially-stable dingo populations is also largely unknown because most dingo populations are persecuted, and most studies have been conducted in persecuted regions (Wallach *et al.*, 2010). The limitations of the data used in this study, overall, likely overestimates prey ranges for extinct species, while underestimates them for dingoes.

Recognizing prehistorical extinctions provides important ecological and evolutionary context to our understanding of seemingly novel community structures and the web of interactions in which species are embedded (Barnosky *et al.*, 2017). When prehistoric predator community and food web structures are recognized, recently established mammals, where predators are protected, rewire food web structures to resemble those before human-induced extinctions. However, further research is required to understand ecological dynamics in Australian mammal communities, particularly where dingoes are protected, alongside recently established megafauna, and smaller predators and prey. Overall, our findings encourage consideration that species already established within complex ecosystems, including those typically associated with extinctions, can rewire the structure of otherwise simplified food webs and restore trophic complexity to ecosystems.

CHAPTER 7 | General discussion and synthesis

“One way to open your eyes is to ask yourself, ‘What if I had never seen this before? What if I knew I would never see it again?’”

Rachel Carson

7.1 | Summary of overall findings

By learning from past ecological communities, prior to human impacts, this thesis explored the extent to which ecosystem trophic complexity with carnivorous mammals could be restored in the Anthropocene. Human-driven defaunation resulted in the reduced distribution of large-bodied hypercarnivorous mammals today. As a result, continental ensemble structures of native carnivorous mammal species are highly modified compared to what they would be today without past human impacts, with the Australian ensemble being the most modified (*Chapter 2*). As a passive approach to reversing defaunation, facilitating natural recolonisations of hypercarnivores would ensure defaunated assemblage structures are restored across Africa, much of Eurasia, and partially for North America, in particular restoring pursuit predators (*Chapter 3*). The trait data used to describe diet compositions in these chapters, however, were limited for investigating opportunities to actively restore trophic complexity at finer spatial resolutions, so I created CarniDIET, an open-access database containing geo-referenced diet records for carnivorous mammals at the population-level (*Chapter 4*). Using CarniDIET, I found that existing knowledge of species interactions could facilitate widespread opportunities for future evidence-based reintroductions of carnivorous mammals (*Chapter 5*). Finally, I demonstrated that former introductions have reversed structural modifications to the Australian carnivore community and rewired mammalian food webs (*Chapter 6*). However, the capacity for rewired food web structures to resemble those before extinctions is limited by widespread persecution of dingoes, which are Australian ecosystem’s apex predator. Overall, by combining lessons from past ecological communities and species distributions, alongside a novel interaction database, I demonstrate that trophic complexity could be restored to Anthropocene ecosystems

through a combination of passive recolonisations, evidence-based reintroductions, and cautious acceptance of recently established species while protecting apex predators.

7.2 | Contributions to ecological knowledge

The results presented in this thesis address key knowledge gaps that present challenges to the widespread restoration of trophic complexity in the Anthropocene. First, learning from the past, in combination with trait-based approaches, reveals a more severe and larger geographic extent of trophic downgrading than previously reported. Second, acknowledging the context-dependence of ecological processes and dynamics suggests existing ecological knowledge may currently limit the geographic scope for trophic rewilding opportunities because of contextual bias in research. Third, recognizing past ecological community structures reveals important ecological and evolutionary context to the roles of introduced species in seemingly novel ecosystems.

Increasing taxonomic inclusivity in trophic downgrading studies revealed a greater extent to trophic downgrading than previously reported. Widespread trophic downgrading of carnivores has previously been demonstrated, although with a focus on species of *Carnivora* $\geq 10\text{kg}$ (Dalerum *et al.*, 2009; Miranda, Parrini & Dalerum, 2013; Wolf & Ripple, 2017). However, these past studies overlooked the need to include species contributing to shared ecological processes when studying community disassembly patterns as opposed to their taxonomic identity (Dehling & Stouffer, 2018). I demonstrated that incorporating species of non-carnivoran mammals into these analyses, including those that only rarely function as carnivores (e.g. snowshoe hares; Michael *et al.* 2018) and commonly (e.g. carnivorous marsupials; *Dasyuromorphia*, *Didelphimorphia*), reveals structural modifications to carnivorous mammal ensembles were most severe in Australia. In contrast, by focusing on taxonomic identity alone, previous functional ecology studies (e.g. Dalerum *et al.*, 2009; Dalerum, 2013) overlooked the continent with the most severe extent of trophic downgrading which requires recognition to ensure effective conservation actions are prioritised and implemented.

The capacity to address questions on ecological community structures and context-dependent dynamics across large spatial and temporal scales, all of which are crucial considerations for rewilding, will depend upon the development of open-access databases of species traits and their ecological interactions driving ecological processes.

Such resources would also benefit from a wide taxonomic inclusivity to ensure their geographically widespread use for conservation. For example, a recent database demonstrated this capability by collating functional traits for herbivorous birds and reptiles, alongside mammals (Lundgren *et al.*, 2021c). For this thesis, I established two databases: one of functional traits that influence the predatory effects of hypercarnivores and another of population-level interactions formed by carnivores (CarniDIET). These databases allowed questions for species across taxonomic groups to be addressed by incorporating functional traits or quantitative trophic interactions (i.e. ‘diet records’) for mammal species that share ecological processes they contribute to. These databases can also be combined with various other functional trait databases (Wilman *et al.*, 2014; Faurby *et al.*, 2018; Lundgren *et al.*, 2021c) and will be useful for diverse conservation initiatives aimed at restoring ecosystem trophic complexity, including species functional recovery assessments or planning trophic rewilding efforts (Seddon *et al.*, 2014; Pires, 2017; Akçakaya *et al.*, 2020).

Acknowledging the environmental contexts from where ecological interactions are known reveals widespread opportunities to restore trophic complexity through evidence-based forecasting of reintroduction outcomes that could facilitate trophic rewilding with carnivorous mammals. Recognizing relevant, context-specific knowledge for forecasting reintroduction outcomes is crucial for trophic rewilding as a key barrier to implementing it at large spatial scales involves concerns around unexpected ecological outcomes (Nogués-Bravo *et al.*, 2016). Ensuring predictions of ecological outcomes following species reintroductions are realistic could increase support for trophic rewilding projects by using context-specific knowledge of species interactions relevant to the proposed reintroduction site (Baker *et al.*, 2017; Pires, 2017). In doing this, I also found that existing knowledge of species’ ecological interactions represent species’ geographic ranges less than expected given their study effort. This was somewhat expected because ecological studies (Martin *et al.*, 2012), and conservation evidence more generally (Christie *et al.*, 2020, 2021), are known to be geographically biased. Regardless, opportunities to restore trophic complexity through evidence-based trophic rewilding are geographically widespread in the Anthropocene.

Finally, acknowledging the extent of past trophic downgrading, and variation in species’ ecological interactions, reveals that, in some contexts, species that recently established following unintentional introductions may present opportunities today to

restore trophic complexity. While introduced species may not necessarily be ecological replacements of extinct species, the structure of the overall interaction network in which they establish may share properties with that of the past. Such opportunities are particularly true in contexts where apex predators are protected and able to establish top-down interactions that mediate the effects of co-occurring species (Wallach *et al.*, 2015b). If such things were acknowledged for mainland Australia, seemingly novel food webs in ecosystems today share marked resemblance to those before extinctions which would otherwise be highly simplified following extinctions. Such results directly contradict general views that these non-native predators are solely drivers of extinctions that require continued intensive management by humans (Simberloff, Parker & Windle, 2005). These typical views likely emerge from contemporary food webs being more highly connected than those of the past, smaller introduced predator relying more on smaller prey, and because top-down interactions have been widely removed from ecosystems through dingo persecution (Wallach *et al.*, 2015b). However, in contexts with protected dingo populations, the emergent structure of rewired food webs are similar to those that assembled in the absence of human impacts, in the earliest Late Pleistocene, and could be interpreted as having restored trophic complexity and community structure. These findings contribute to a growing body of research suggesting that introduced species have the capacity to restore ecological functions that were lost following extinctions (Tanentzap & Smith, 2018; Lundgren *et al.*, 2020, 2021a, 2021b).

7.3 | Implications for conservation policy and research prioritisation

The research presented in this thesis contributes to the growing recognition that palaeoecological insight, alongside broad-scale macroecological perspectives, can be merged with conservation to advise on environmental challenges in the Anthropocene (Fig 7.1). A macroecological lens has been applied to the topics investigated in this thesis, so the findings of this thesis contribute to applied conservation and management by providing broad-scale perspectives (Santini *et al.*, 2021). Conservationists are also increasingly recognizing that learning from the past can provide insights relevant for conservation today, such as the management of novel ecosystems, and guide future conservation policies (Barnosky *et al.*, 2017; Fordham *et al.*, 2020). Crucially, moving

beyond recent historical baselines (Wolf & Ripple, 2017; Pacifici *et al.*, 2020) can reveal the full extent of humanity's impacts on the structure of ecological communities (Schowanek *et al.*, 2021). For example, using the palaeoecological fossil records reveals that humans have severely modified the structure of ecological communities, that have otherwise remained remarkably consistent for millions of years, and provides necessary ecological and evolutionary context for the prioritisation of conservation resources and ecosystem management today and for future global change (Svenning *et al.*, 2019; Blanco *et al.*, 2021). This includes contextualising the severity of human impacts by showing they are analogous to environmental disturbances that have caused carnivore extinctions throughout geological time. Such findings reinforce the emerging consensus that we need to reduce, and reverse, our impacts today for the future evolutionary trajectory of life on Earth (Davis *et al.*, 2018).

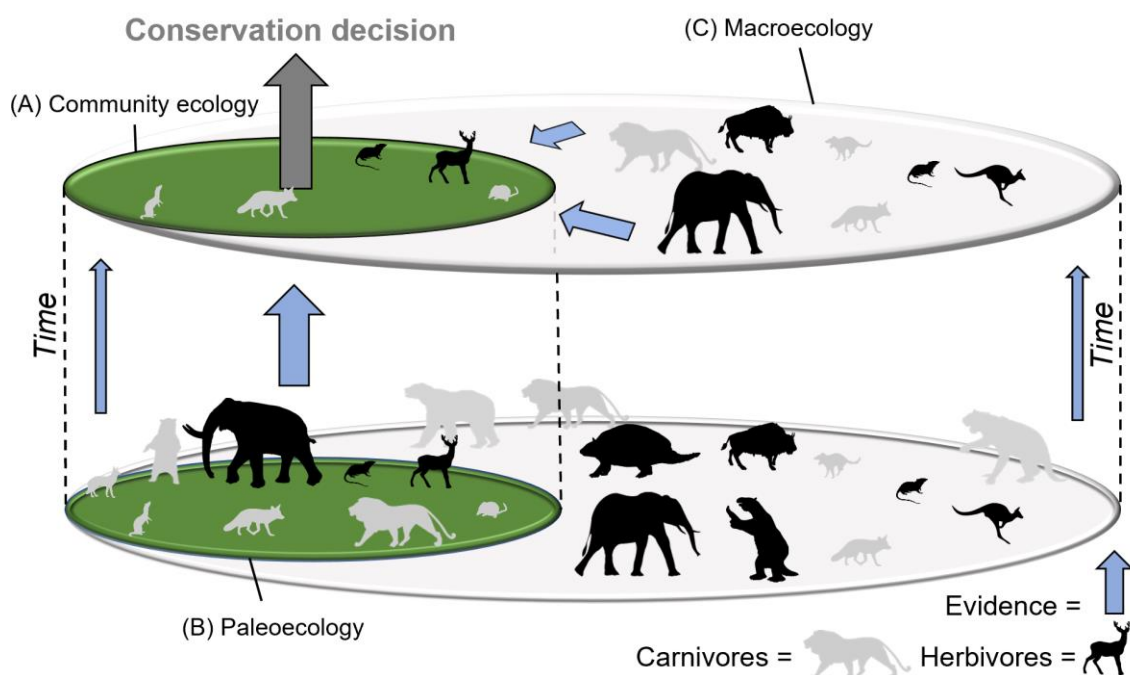


FIGURE 7.1 | Evidence available for conservation by recognizing ecological community structures at palaeoecological and macroecological scales. The green circle represents a mammal community in the United Kingdom, while the grey circle does not reflect a specific location but includes extinct and extant species that have occurred across the world since the earliest Late Pleistocene. (A) Traditional studies of ecological communities (e.g. monitoring abundance, densities, and species interactions) can help inform conservation actions. (B) Palaeoecological insights reveal former ecological community structures prior to human impacts and can reveal missing ecological functions. (C) Macroecological insight can reveal generalised patterns in ecological community structures, disassembly patterns, and stimulate discussions around broad-scale conservation initiatives that are implemented at local scales.

Restoring trophic complexity through species reintroductions in trophic rewilding projects will need to recognise justified concerns that unforeseen ecological effects could occur through unanticipated ecological interactions emerging. To overcome such concerns, trophic rewilding advocates recommend following the IUCN's translocation guidelines which requires best available data to be used in risk assessments to facilitate evidence-based decisions (IUCN/SSC, 2013). Predictive forecasting of species reintroduction outcomes could form a part of this assessment and would be most evidence-based when knowledge of species ecological interactions are applied from comparable environmental contexts to the proposed reintroduction site (Pires, 2017). Therefore, going forward, conservation research could prioritize unstudied environmental contexts to increase the geographic scope for evidence-based trophic rewilding opportunities further. While the most common ecological interactions that species form in ecosystems are well-known, even weak and rare interactions could influence ecosystem functioning and deserve recognition to avoid concerns (e.g. Nogués-Bravo *et al.*, 2016) by using context-specific knowledge in forecasting species reintroduction outcomes (Berlow, 1999).

By learning from the past, conservation efforts are increasingly suggested to require shifting from taxonomic compositions to functional ecological community structures and ecosystems to safeguard biodiversity under future global change (Barnosky *et al.*, 2017; Perino *et al.*, 2019). Shifting to a functional focus in conservation could be achieved by focusing on 'taxon-free' metrics, including species functional traits, trophic structures, and interaction networks (Harvey *et al.*, 2017; Perino *et al.*, 2019; Akçakaya *et al.*, 2020). However, this would require certain non-native species recognised as having conservation value within seemingly novel ecosystems, for example by international conservation groups (e.g. IUCN) recognizing them in conservation assessments (e.g. dingoes; Wallach *et al.*, 2020). Using taxon-free metrics revealed that the structure of the contemporary Australian carnivore assemblage resembled those before extinctions, which follows long term palaeoecological trends of structural consistency despite turnover in taxonomic identity (Blanco *et al.*, 2021). However, the Australian government has recently awarded £214,500 to continue the National Wild Dog Action Plan between 2020-2030, a large-scale coordinated lethal-control programme of dingoes. As such, the potential to restore trophic complexity and resilient, functional ecological community structures in Australia remains uncertain. Conservation policy could alternatively focus

on protecting ecological community structures and prioritising the protection of dingoes which has been widely argued in the past decade (Johnson *et al.*, 2007; Letnic & Koch, 2010; Wallach *et al.*, 2010; Letnic *et al.*, 2012b; Colman *et al.*, 2014) and could be facilitated through predator-friendly farming (Johnson & Wallach, 2016; Wallach, Ramp & O'Neill, 2017b).

An increased appreciation of context-dependent ecological dynamics could be applied to ecological knowledge in general which would reveal the extent to which conservation policy implementation is evidence-based (Chamberlain, Bronstein & Rudgers, 2014; Early & Keith, 2019). As such, policy-makers should recognise that certain conservation policies and decisions are not automatically generalizable across the range of environmental contexts they would be implemented. For example, context-dependencies influence the outcome of non-native species eradication programmes that receive a large amount of limited conservation resources and can sometimes further conservation issues (Rayner *et al.*, 2007; Bergstrom *et al.*, 2009; Courchamp *et al.*, 2011). A potential emerging example of this, is the ongoing donkey removals in the southern US despite research showing their importance as a prey resource for highly persecuted puma populations (Lundgren *et al.*, 2021a). Recognizing context-dependence would also benefit future research prioritization efforts to increase species-specific ecological knowledge in general which may be skewed through geographically-biased research (Britnell *et al.*, 2021). Such a phenomena has likely occurred with Eurasian lynx (*Lynx lynx*) becoming stereotyped as a specialist of ungulates because research has focussed in Western Europe, while recent research in Eastern Europe, and other locations, demonstrates their preference for brown hares (*Lepus europaeus*) despite also co-occurring with ungulates (Mengüllüoğlu *et al.*, 2018). Further, contrary to typical perception of their ecological niche, snowshoe hares have been documented scavenging animal biomass (Michael *et al.*, 2018) and grey wolves, can have diets consisting almost entirely of fruit at certain times of year (Gable & Windels, 2018). Conservationists should therefore strive to ensure knowledge of species' ecologies becomes representative across the range of environmental contexts in which they occur to identify any degree of plasticity in their traits and ecological functions (Britnell *et al.*, 2021).

7.4 | Limitations and recommendations for future research

Understanding the functional implications of modifications to mammal communities across the world by humans has heavily relied upon the use of counterfactual distributions today for all mammals that existed during the late Quaternary in the absence of long-term humans impacts (Faurby & Svenning, 2015; Fig. A2.1). Counterfactuals are increasingly used to in conservation to contextualise outcomes by comparing observed patterns to outcomes from alternative realities (Grace *et al.*, 2021), which in this case of this thesis is through exploring the potential range of all late Quaternary mammals today. The ‘present-natural’ maps from Faurby & Svenning (2015) are also frequently used as a proxy for mammal distributions during the last interglacial (~125,000 years ago) which is typically justified by the two interglacial periods have similar climates. An alternative method of constructing species prehistorical distribution would be through combining current and fossil occurrence records with the associated climate variables to predict former distributions from a time with known climatic conditions (e.g. McGuire & Davis, 2013). Such methods could, arguably, be advantageous but the fossil record would be skewed towards larger species and unlikely reflect their full former distribution. Regardless, the method of fossil co-occurrence mapping by Faurby & Svenning (2015) was found to accurately predict the known distribution of North American mammals before the arrival of Europeans. Despite uncertainty in these counterfactual distributions as a proxy for the past, even typically accepted current species distribution maps unlikely reflect reality, for example by including areas in between known populations in which species do not occur (Graham & Hijmans, 2006). At macroecological scales, as used throughout this thesis, such biases are typically accepted to average out across species and regions.

Throughout this thesis, species diets are heavily relied upon as a key trait that determines their ecological functions. Species diets are central to describing a species biology, alongside body mass (Price & Hopkins, 2015), and their role in interactions networks within ecosystems. However, the direct trophic interactions that form species’ diets are only a subset of the traits that fully describe species’ ecological effects within ecosystems. For carnivores, understanding how dietary variation translates to variation in the strength of their indirect interactions on prey species, through fear-induced behavioural modifications, will be fundamental for determining their context-dependent ecological functions in practice (Wirsing *et al.*, 2020). For species beyond carnivores, other

behavioural traits, including spatial patterns of a population's movement (e.g. seasonal migration), would further modify species' ecological functions and contributions to ecological processes in an area (Akçakaya *et al.*, 2020). A limitation to the results in this thesis, and a recommendation for future research, would be the need to incorporate more data that further describe species' ecological functions.

Data resolution also presented limitations to the analyses in this thesis in various ways. Diet compositions described by low resolution categories (e.g. vertebrate, invertebrate, and plant; % consumed) broadly capture, alongside body mass, their position in food webs (Price & Hopkins, 2015). However, higher resolution diet categories (see EltonTraits, Wilman *et al.* (2014)) could reveal more subtle patterns of community disassembly, although with the trade-off being greater uncertainty surrounding the diet traits of extinct species. Such limitations were a key driver for creating CarniDIET, although limitations also exist here. Crucially, diet records cannot currently be attributed to scavenging or predation events, something that differentiates the ecological processes species contribute to. In Chapter 4, I overcame this by merging CarniDIET records with the maximum prey size observed hunting of each predator, which can be done using the Global Biotic Interactions database (Poelen *et al.*, 2014).

CarniDIET presents an opening to macroecological and macroevolutionary research but further data collation should ensure taxonomic and demographic resolutions are improved alongside additional coverage across species' geographic ranges (as recommended in Britnell *et al.*, 2021). Such improvements would facilitate higher resolution of community disassembly analyses and a greater appreciation of the variability of species ecological roles in food webs. Another logical step would be to integrate more species into the database that are beyond what we define as 'mammal-consumers', which would include other species of *Mammalia* as well as non-*Mammalia*. Such a recommendation is echoed throughout this thesis, which demonstrated the need to be taxonomically inclusive of species contributing to shared ecological processes in studies of functional diversity and ecological community structures, as suggested by Dehling & Stouffer (2018).

The quantitative interaction data available in CarniDIET would make a start for predicting the outcomes of species reintroductions using context-specific evidence (Baker *et al.*, 2017; Pires, 2017). However, additional data beyond species diets and body mass

would be required to do this effectively, for example population densities. Population density scaling laws have been widely studied (Pedersen, Faurby & Svenning, 2017) with recent work showing that humans are modifying these relationships and could be incorporated into macroecological analyses (Santini & Isaac, 2021). Population density estimates for species across their geographic range are also widely available in an open-access database TetraDENSITY (Santini *et al.*, 2018). This database, alongside CarniDIET, and another on life-history strategies (COMADRE; Salguero-Gómez *et al.* 2016), could provide the necessary data for predicting trophic rewilding outcomes following species introductions at fine scales given data availability from comparable environmental contexts.

While limitations in diet knowledge may occur across species' geographic ranges, CarniDIET could be used to fill such gaps across their geographic ranges. Predictive modelling could be performed to infer diets, and species' contributions to ecological processes, across large spatial scales using key environmental variables that drive variation in species' diets (as in Woinarski *et al.* 2017). Latitude, for example, is known to influence the proportion of carnivory in omnivorous species (Vulla *et al.*, 2009). High levels of human impacts also influence prey availability to predators, so that prey consumed by large predators are smaller closer to human settlements than further away (Henschel *et al.*, 2011). As many species display seasonal variation in resources consumed, areas in species' ranges with higher seasonality could have high variability in a species' diet than less seasonal areas (Davidson *et al.*, 2013; Aleksandra & Duško, 2015; Murray *et al.*, 2017). Alternatively, such predictions may be unnecessary if species' diets are predictable and consistent across geographic ranges, which I highly recommend being investigated. Ecoregions are nested within biomes, and capture areas with broadly similar environmental conditions with similar ecological communities (Olson *et al.*, 2006). As environmental conditions and species compositions can influence species' diets, it is likely that ecoregions could form a realistic unit in which a species' diet would be largely consistent. It could be hypothesised that the taxonomic composition of species diets between ecoregions may vary but the composition of broad food categories, including traits of those resources (e.g. prey species traits), may be similar. The results of such analyses could determine if species have similar ecological functions across their geographic ranges, using similar methodologies as in Smith *et al.*(2018c).

If predictive modelling of species' diets were found to be reliable, the capacity for extinct species diets to be predicted could be explored, which is something that remains surrounded by uncertainty. If possible, further research could use the methods in Chapter 4 to reconstruct past, present, and future biome or ecoregion food webs across continents using CarniDIET, alongside maximum prey body mass size from GloBI (Poelen *et al.*, 2014). In doing so, future scenarios could be designed and evaluated based on varying levels of human-impacts. Species' extinction probabilities, according to their threat status (as implemented in: Davis *et al.* 2018a; Cooke *et al.* 2019), could then be calculated followed by random extinctions of predator and prey species to identify how future defaunation scenarios could impact global food web structures. Further, simulations of unintentional introductions or intentional reintroductions of species would reveal how future trophic rewilding could alter, and potentially restore, food web structures.

Extensive uncertainty remains around the context-dependent effects of introduced species across the variety of environmental contexts they now occur in. While the results presented in *Chapter 4* suggest introduced mammals have the capacity to rewire interaction network structures, this requires investigation through further fieldwork that cannot be answered using macroecological trait-based modelling. For example, dingoes are known to be able to regulate populations of red kangaroo (Letnic, Baker & Nesbitt, 2013) but their capacity to do so with larger introduced ungulates remains unknown, other than, to an extent, sambar deer (*Rusa unicolor*) (Forsyth *et al.*, 2018b, 2018a). However, recent research documented a trophic cascade resulting from a native predator predating on a juvenile non-native herbivore (Lundgren *et al.*, 2021a), meaning adult body mass may not be a limiting factor. The capacity for dingoes to drive a similar trophic cascade with the largest introduced herbivores is unknown. Field research involving large-scale studies around ecosystem dynamics in areas with and without novel species across multiple trophic levels could help unravel such mysteries. To understand further unknown ecological dynamics, research on introduced species could become more open-ended in general, as opposed to following the typical narrative of the harm they cause (Schlaepfer, Sax & Olden, 2011). This thesis focussed on introduced mammals in Australia, but such considerations are applicable to introduced species more widely. For example, recent work has shown the rapid evolution of foxgloves (*Digitalis purpurea*) to hummingbirds (Family: *Trochilidae*) as a novel pollinator functional group (Mackin *et al.*, 2021), and

that introduced donkeys can provide access to water for species in dryland ecosystems (Lundgren *et al.*, 2021b). If these introduced species were simply removed without study, such interesting evolutionary and ecological dynamics would remain unknown.

7.5 | Concluding remarks

Reversing past human-induced trophic downgrading could be achieved through multiple pathways. First, facilitating natural recolonisations by maximising landscape connectivity would be the most nature driven approach to restoring ecological community structures. Second, existing knowledge could be used to forecast the potential outcomes of species reintroductions to assist evidence-based trophic rewilding. Finally, and arguably most controversially, past introductions could be evaluated to determine if they could be restoring trophic complexity and structure to ecological communities. At this crucial junction for conservation, the beginning of the UN's Decade on Ecosystem Restoration, these are viable options for the immediate future and are central to restoration discussions. Expanding the focus of conservation and restoration to consider species ecological functions and past ecological dynamics would help facilitate the recovery of trophic complexity and in turn the improved functioning and resilience across the world's ecosystems.

Overall, this thesis explored diverse opportunities to restore trophic complexity across the world to reverse past, and ongoing, human-induced defaunation and trophic downgrading in the Anthropocene. This research presents a useful resource for Anthropocene ecologists that are ambitious and hopeful in restoring ecosystem trophic complexity through evidence-based decision making. With wildlife rapidly diminishing, protecting what we have and making the most of the available opportunities today will be vital to safeguard biodiversity that will otherwise take millions of years to recover.

8 | Bibliography

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9.1 | Chapter 2

9.1.1 | Figures

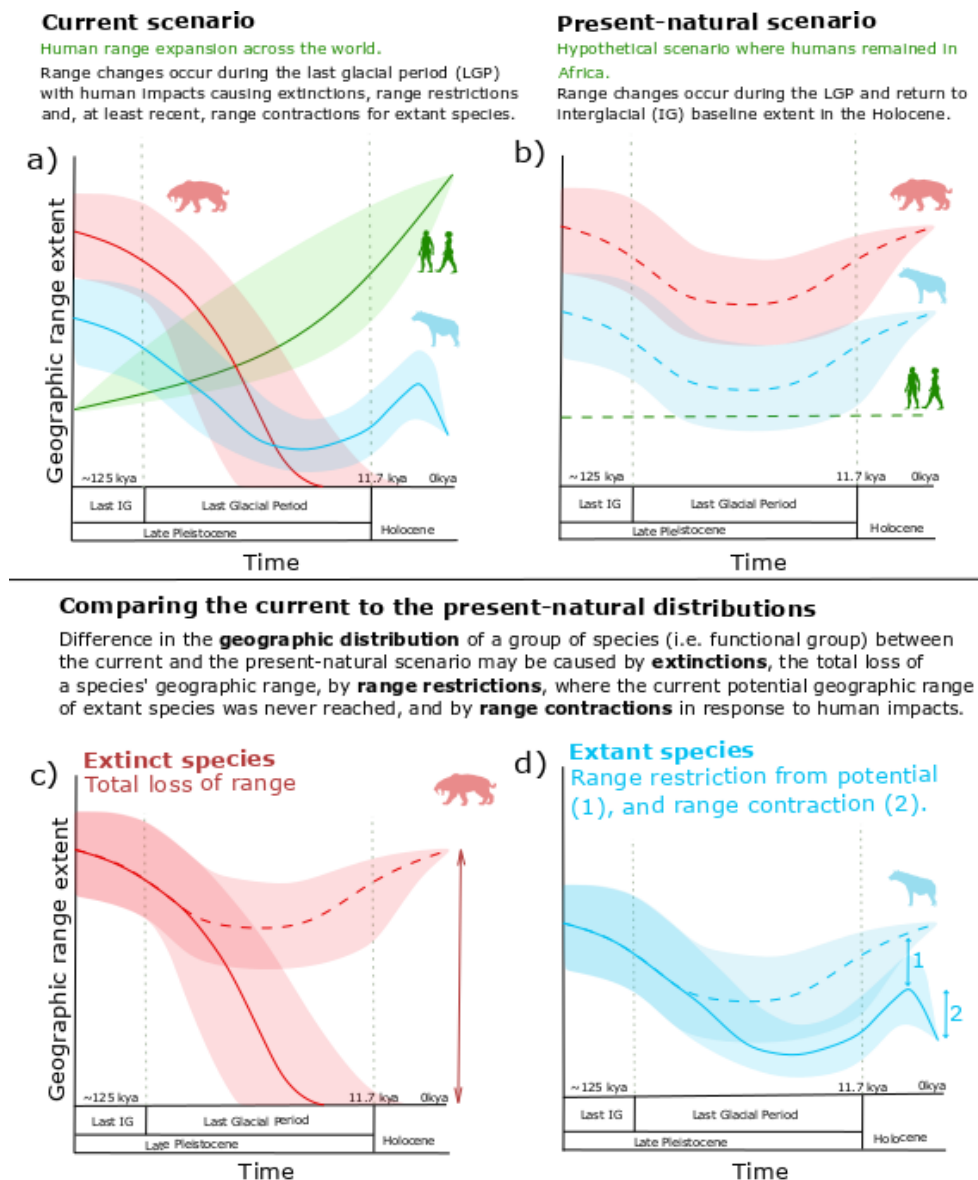


FIGURE A2.1 | Conceptual diagram comparing the geographic ranges of species between the present-natural (PN) and the current scenario. (a) In the current scenario, extinctions occurred during the Late Pleistocene and Holocene, as well as range restrictions and, at least recently, human-induced range changes for extant species. These were caused by the combined effects of changing climate and the widespread presence and impacts of humans, following the migration

out of Africa during the Late Pleistocene. (b) In the present-natural scenario, modern humans (*Homo sapiens*) did not leave Africa, although the geographic ranges of mammals are still altered by changing climates during the last glacial period (~130 – 11.7kya). Due to the absence of widespread modern human impacts, all mammal geographic distributions return to a roughly interglacial baseline during the Holocene through natural recolonization. The present-natural maps therefore represent the distribution of mammals today in the absence of humans outside of Africa, which would likely be similar to the last interglacial, although there remains uncertainty around the last interglacial range size. (c) The difference in the geographic range size for extinct species, between the present-natural and current range maps, is the loss of the potential range of those species today had they not gone extinct. (d) The difference in the geographic range size for extant species, between the PN and the current, involves a combination of geographic range restrictions from their potential range today, as well as direct geographic range contractions through, at least recent, human impacts. The combination of these processes will vary depending on the history of each species. These diagrams are hypothetical examples to illustrate the concept for exemplary extinct (red) and extant (blue) species (*Smilodon fatalis* and *Crocota Crocota*, respectively). We are not attempting to reflect the actual range variation through the late Quaternary of these species. Further, the geographic range size for humans (green) relative to the other species' range sizes is not comparable, and merely illustrates the direction of change in range extent.

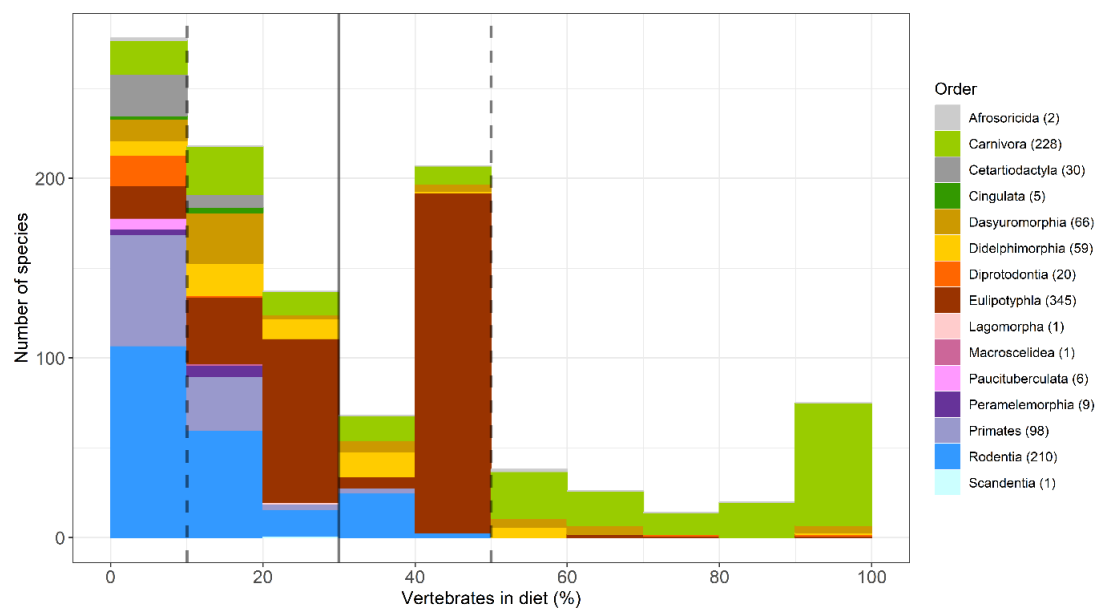


FIGURE A2.2 | Number of carnivorous mammals in bins of vertebrate biomass consumption. The frequency of terrestrial, carnivorous native mammals that fit the selection criteria ($n = 1,081$ species) distributed by the percentage of vertebrate meat in their diet by 10% bins. Colours represent orders of Mammalia. The solid line indicates the median dietary traits of species included in the analysis (30%), and dashed lines indicate the lower (10%) and upper (50%) quartiles.

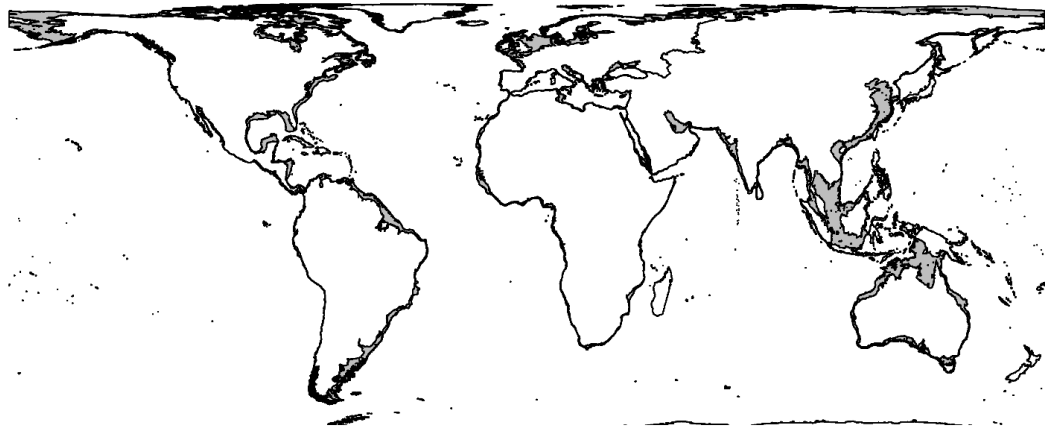


FIGURE A2.3 | Current-day land mass compared to the Glacial maximum land mass. Current land mass is divided by continents, above the shapefile of the global land mass at 110m below sea level (grey), as it was during the last Glacial Maximum. This shows which islands were connected to the continental mainland at some point throughout the Late Pleistocene, with sea levels ~110m lower than present. The Pleistocene land mass shapefile was created using bathymetry data and including grid cells which are 110m below sea level.

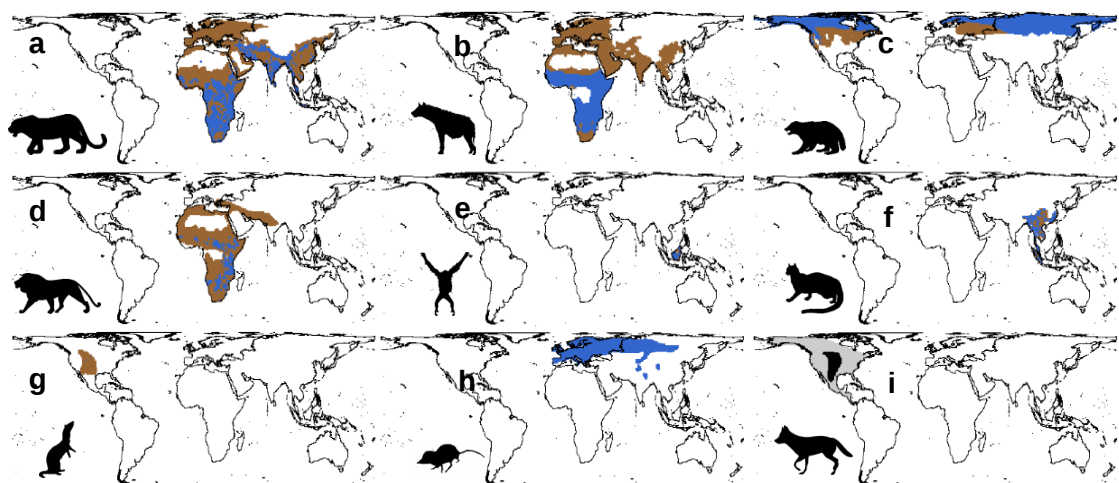


FIGURE A2.4 | Geographic ranges of nine species showing examples of how the current range (blue in a-h; black and grey in i) differs from the present-natural range (brown and blue in a-h; black in i). Differences primarily consisted of range reductions (a-h), although range expansions did occur, e.g. coyote *Canis latrans* (i), where the current range (black and grey) is larger than the present-natural range (black). a) Leopards (*Panthera pardus*), and b) spotted hyenas (*Crocuta crocuta*) were once widespread across Africa, Asia and Europe, although are now restricted to portions of Asia and Africa. c) Wolverines (*Gulo gulo*) are restricted to high latitudinal areas of North America, Europe and Asia, although have lost large portions of their Southern range, particularly in Europe and North America. d) Lions (*Panthera leo*) are now restricted to highly fragmented regions in Sub-Saharan Africa, although were previously widespread across Africa and into the Middle East and Southern Asia. e) Orangutans (*Pongo pygmaeus*) are endemic to Borneo, although now have a fragmented range in comparison to their once widespread Bornean range. f) The jungle cat (*Catopuma temmincki*) has lost regions of its originally small range in South-East Asia. g) Black-footed ferrets (*Mustela nigripes*) occupied regions of Central-Western North America, although now only occur in a few fragments of their former range. h) The Eurasian shrew (*Sorex araneus*) is an example of a species which has not

undergone range contractions since the last interglacial. i) Coyotes (*Canis latrans*) have undergone range expansions since the last interglacial and are now widespread across North America.

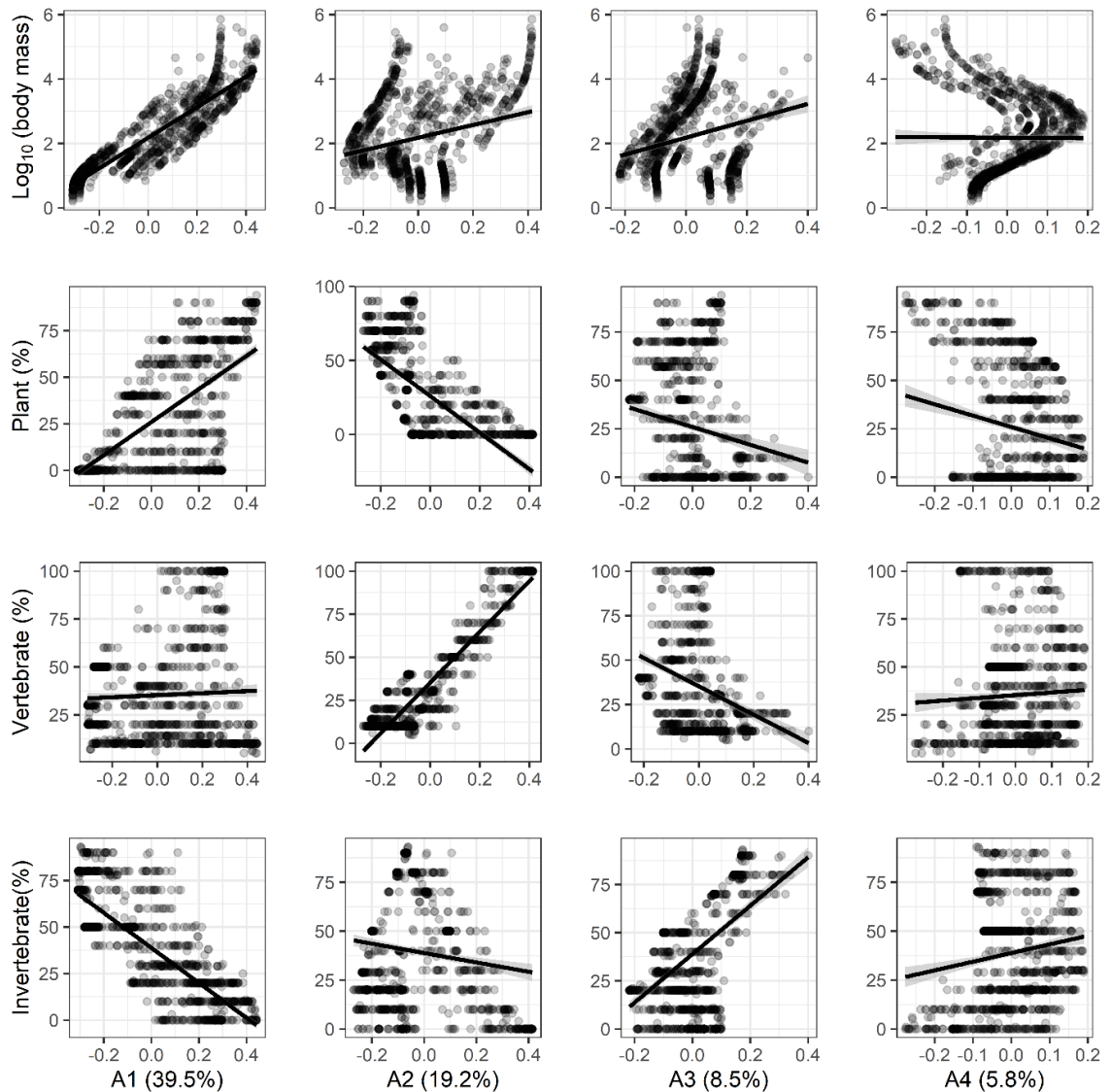


FIGURE A2.5 | Correlations between principal coordinate axes 1, 2, 3 and 4 against original functional traits to show the representation of original traits in functional space. Each of the new principal components (A1-4) has unique axes representing body mass or dietary strategies. A1 positively correlated with plant consumption (%) and log₁₀(body mass, g), and negatively correlated with invertebrate consumption (%). A2 positively correlated with vertebrate consumption (%) and negatively with plant consumption (%). A3 weakly positively correlated with invertebrate consumption and negatively with vertebrate consumption. A4 did not correlate with any original dietary strategies, although low values typically indicate medium-bodied generalists.

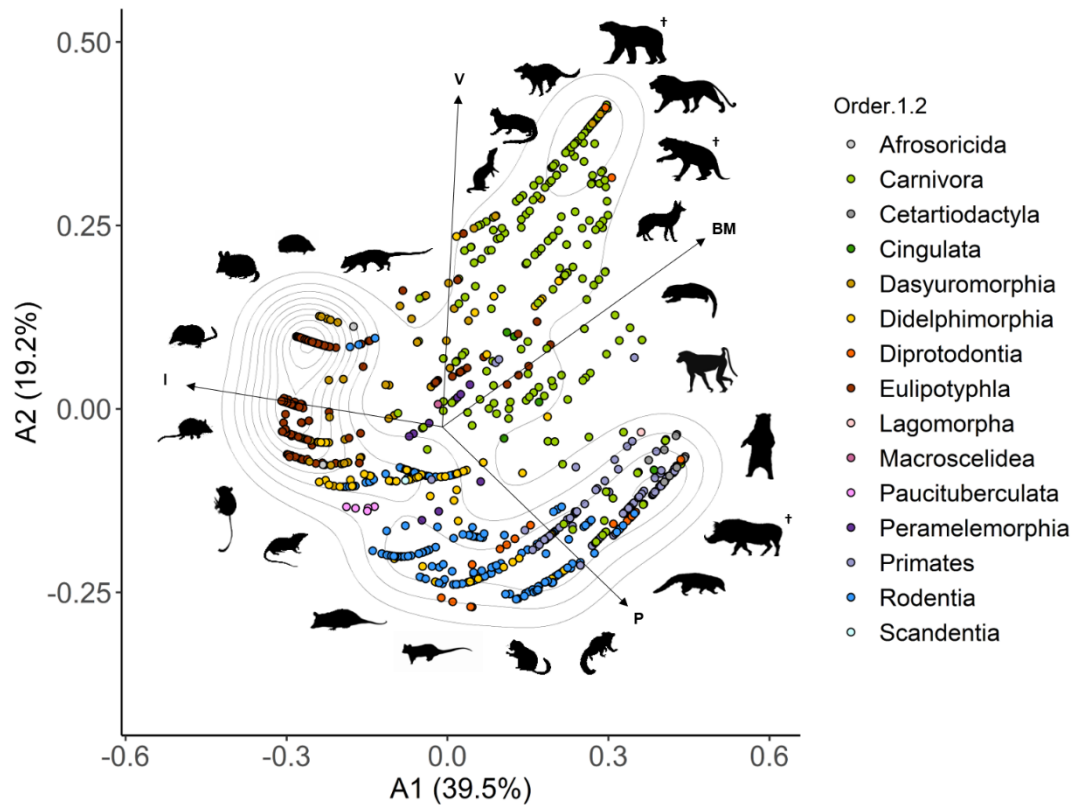


FIGURE A2.6 | Global carnivorous mammal functional trait space in two dimensions. Extinct (†) and extant terrestrial carnivorous mammal species are shown. Arrows indicate a representation of the four original traits (P = plant, I = invertebrate, V = vertebrate, and BM = body mass) in the first two dimensions of traits space. The first four PCoA axes of the global trait space were reduced to principal components with the first two explaining the greatest variation (80%). Colours indicate a species' taxonomic order. Contour lines indicate kernel density lines to represent the distribution and density of species in functional traits space.

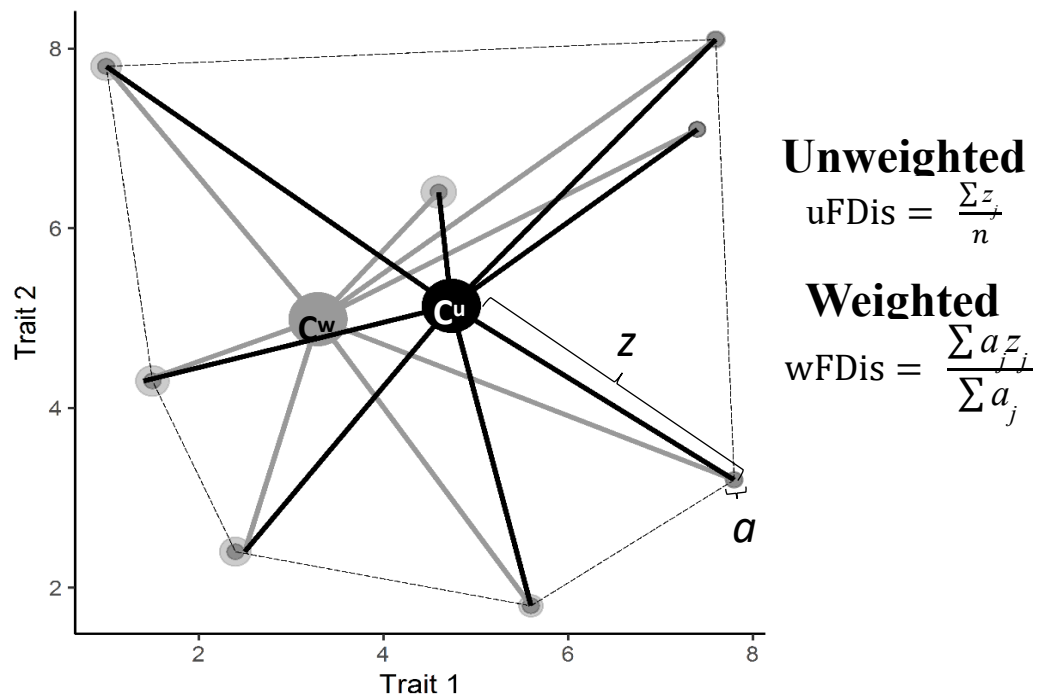


FIGURE A2.7 | Graphical representation of the calculations of functional diversity metrics in functional trait space, following Laliberté & Legendre (Laliberté & Legendre, 2010). Each point represents a species in a given species pool in 2-dimensional trait space, shown as unweighted (black) and weighted (grey) by a given weighting (i.e. abundance or range size). Functional richness (FRic), the minimum convex hull around points (dashed lines) is not affected by weighting, while functional dispersion (FDis), the average distance (solid lines) of all species from the centroid (C), can be influenced by a weighting (in the case of this study, geographic range size). The position of C can change depending on whether species are weighted (C_w) or unweighted (C_u) by a given weighting (i.e. abundance or range size).

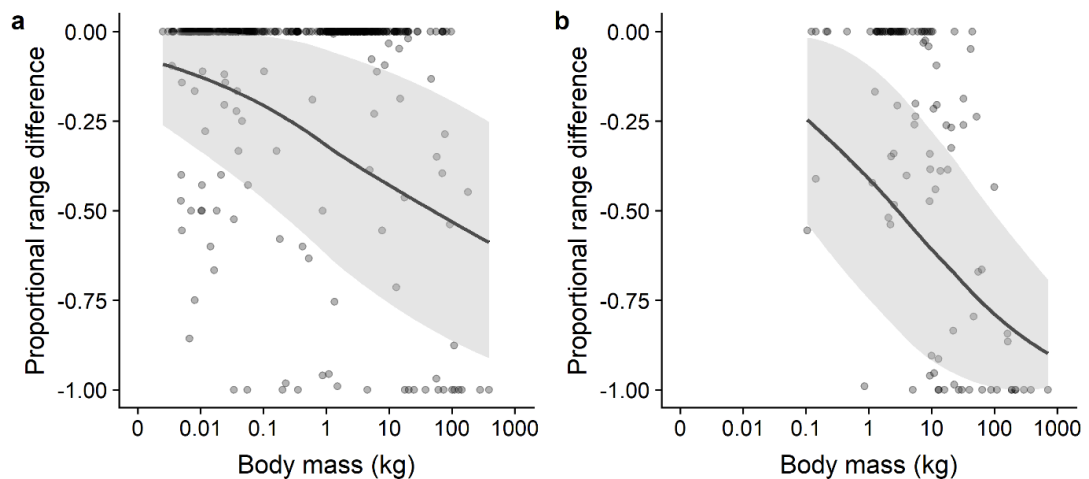


FIGURE A2.8 | Proportional geographic range change for systematically reviewed carnivorous mammals (n = 555). Geographic range change (points with equal transparency) between current and present-natural scenarios increased with greater body masses ($\log_{10}(\text{kg})$ for interpretability). The effect was higher for species with increased vertebrate meat consumption, shown for (a) non-hypercarnivores (5-69% vertebrate meat), and (b) hypercarnivores ($\geq 70\%$ vertebrate meat).

Average BBPMM estimate (black line), accounting for shared ancestry, is shown with upper and lower 95% credible intervals (shaded area).

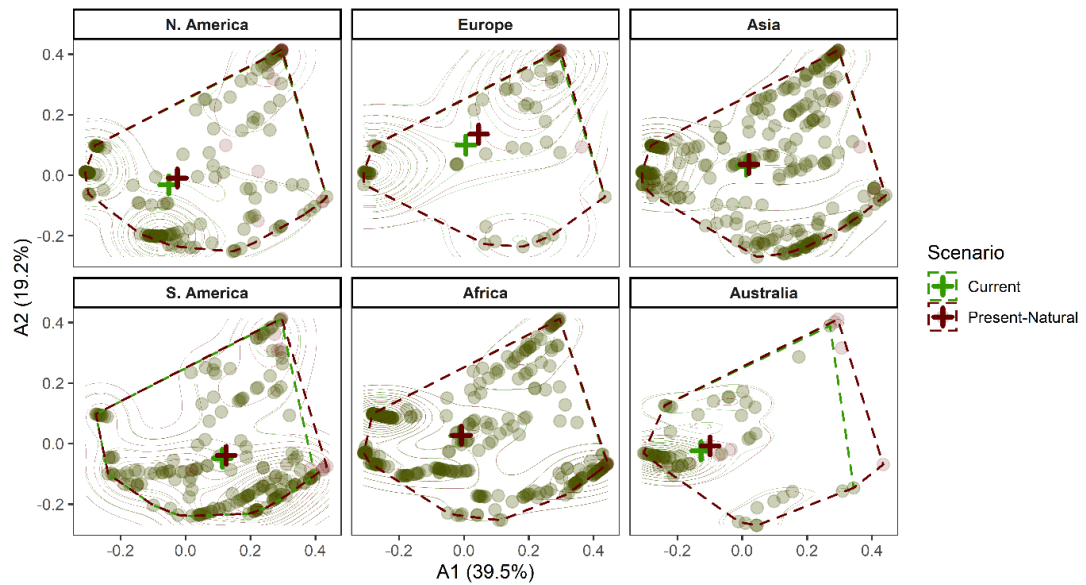


FIGURE A2.9 | Continental functional trait spaces shown in two dimensions with species represented as points which occur in the present-natural (brown) and current (green) ensembles, without geographic range size represented (presence only). Changes in functional richness are shown by minimum convex polygons (dashed lines) for present natural (brown) and current (green) ensembles per continent displayed in two dimensions explaining 59% of the variance. Functional dispersion is represented by the distance of all species from the ensemble centroids (crosses) for present-natural (brown) and current (green) ensembles representing the centres of the functional hypervolumes.

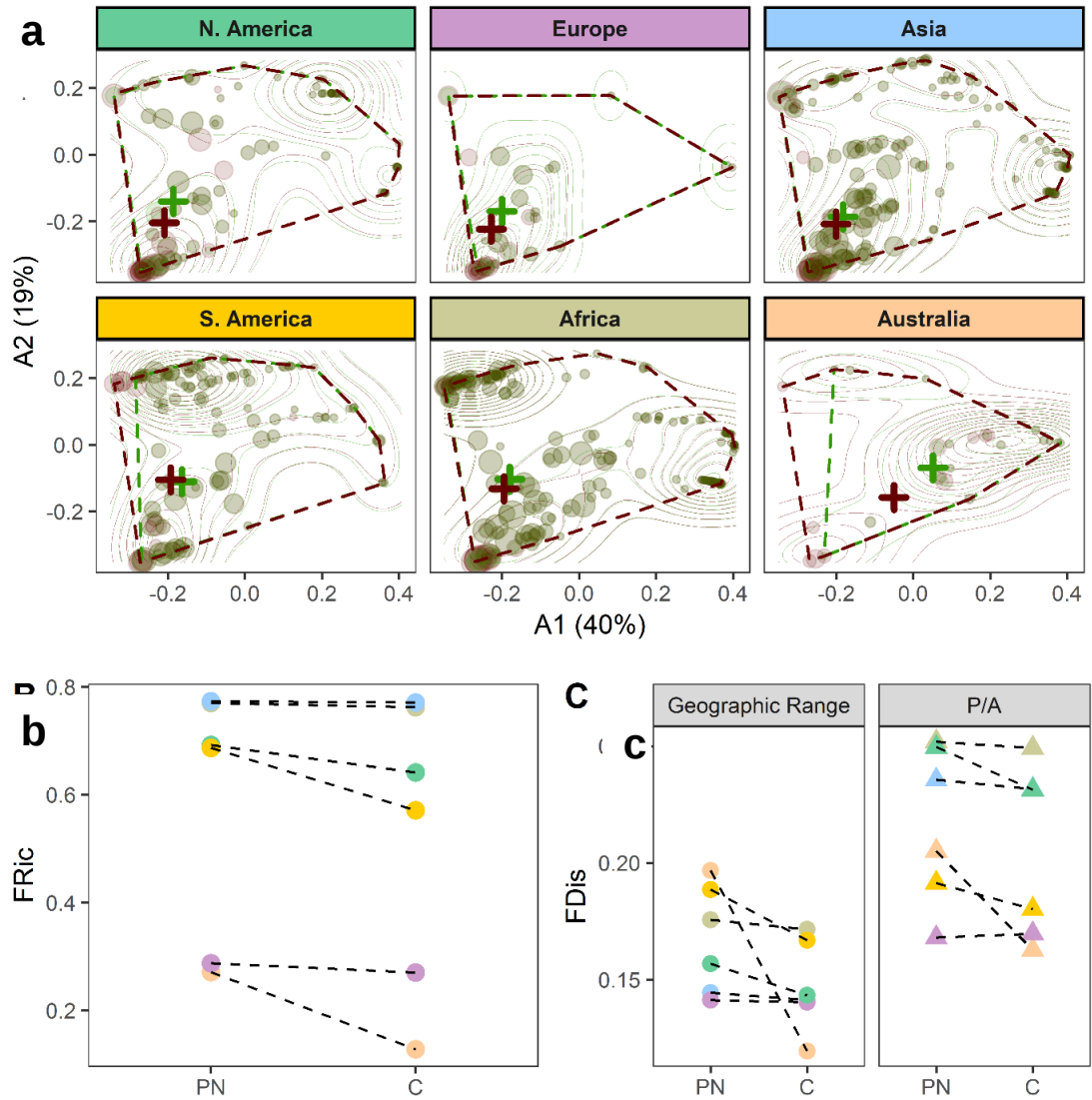


FIGURE A2.10 | Functional diversity differences between the present-natural and current for each continent, using only the systematically-reviewed species ($n = 555$). (a) Continental functional trait spaces (species richness in parentheses) shown using the first two PCoA axes with species represented by points (size scaled to geographic range size) for present-natural (PN; brown) and current (C; green) scenarios. For simplicity, only the first two axes of change in functional richness are shown here by minimum convex polygons (dashed lines) for PN and C scenarios for each continent, explaining 59% of the variance, despite it being calculated from the first four axes. Functional dispersion is represented by the distance of all species from the ensemble centroids (crosses) representing the weighted centres of the functional hypervolumes, with the weight being species' geographic range size. (b) Differences between scenarios in the 4-dimensional functional richness (FRic) for each continent between the PN and C scenarios. (c) Difference in functional dispersion (FDis) between scenarios, across continents calculated using two weighting methods: geographic range-weighted (left, circles) and presence-absence (P/A) only (right, triangles). Colours in b & c represent continents, colours as in a.

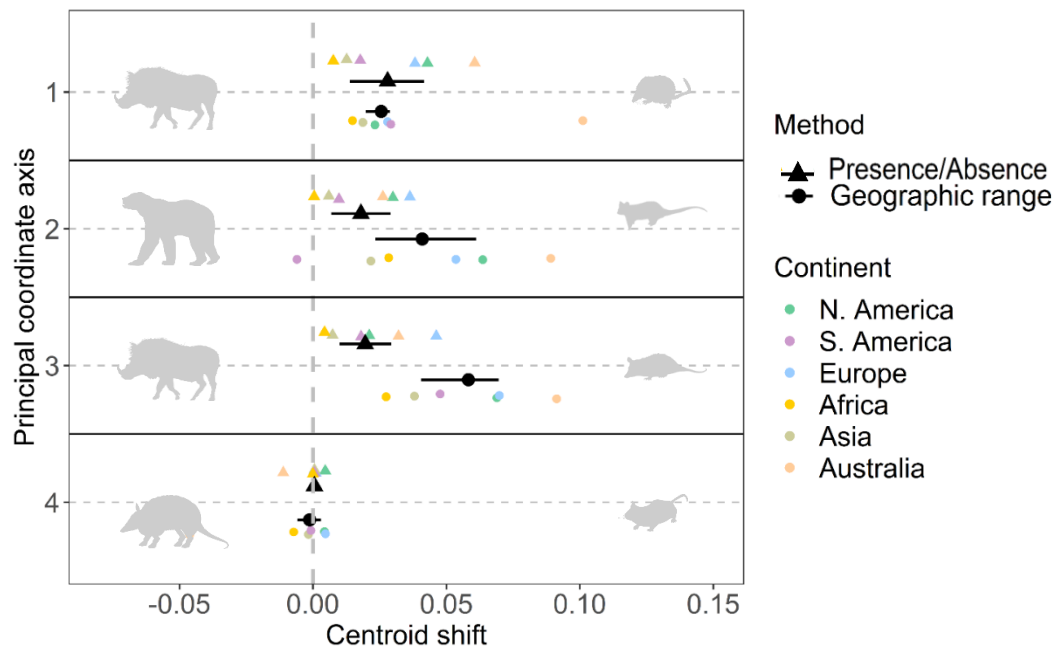


FIGURE A2.11 | The magnitude of the continental ensemble centroid shift from present-natural to current for each continent (colours) along the four axes of functional trait space, using only systematically-reviewed species (n = 555). We used two different weighting methods: with geographic range (circles) and presence-absence (triangles) only. Black points indicate the group median with the interquartile range represented by black lines. Silhouettes highlight species at the extremes of principal components, including from low to high values: *Metridiochoerus compactus* (extinct) to Alaska tiny shrew (A1), *Arctodus simus* (extinct) to long-tailed pygmy possum (A2), *Metridiochoerus compactus* to gray four-eyed possum to (A3), and giant armadillo to montane African climbing mouse (A4). Positive shifts along A1 indicate shifts towards smaller species with generally more insectivorous diets. Positive shifts on A2 indicate shifts away from species with more carnivorous diets. Positive shifts along A3 indicate shifts away from, generally, larger-bodied insectivorous species.

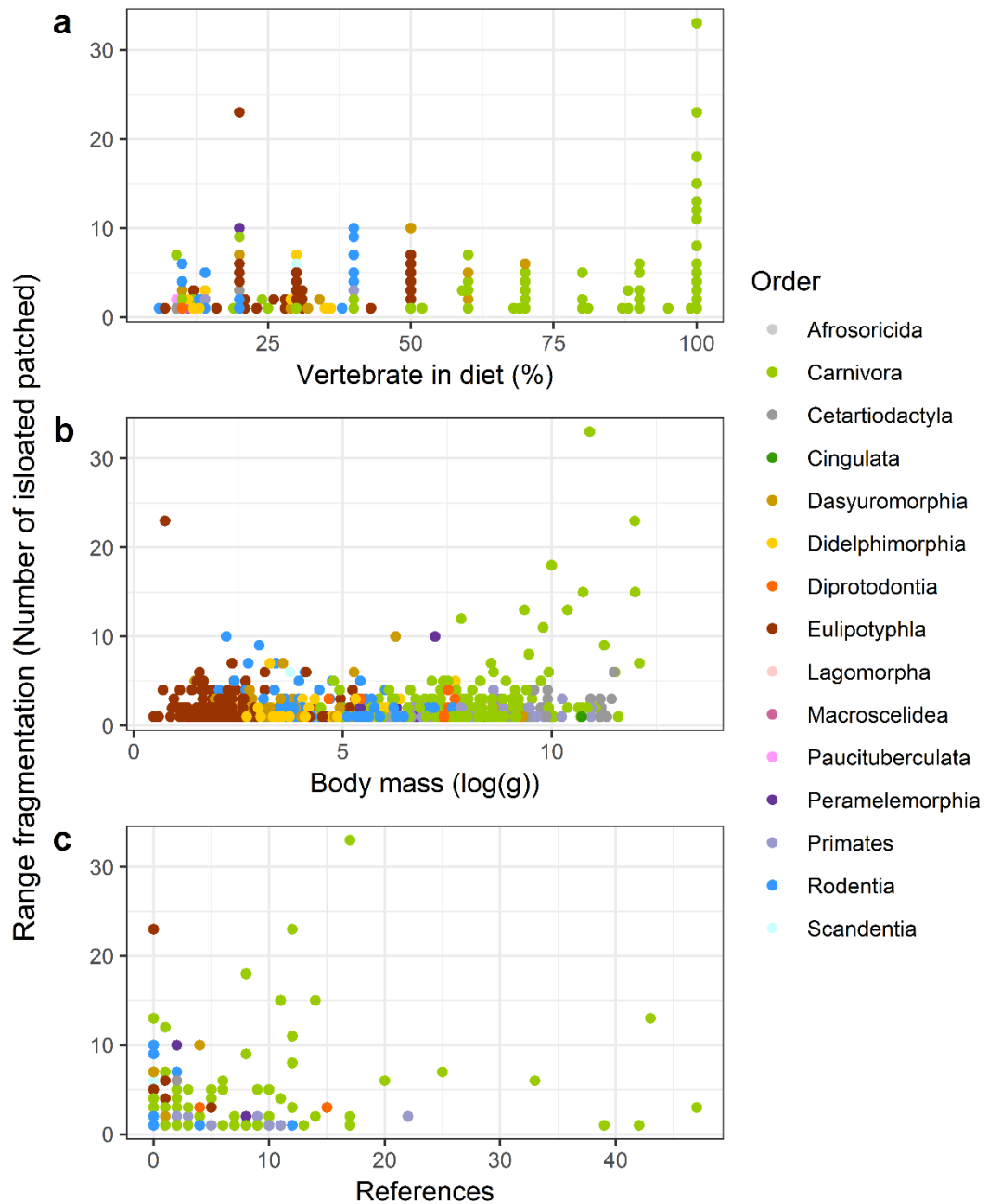


FIGURE A2.12 | Potential correlates of range fragmentation of carnivorous mammals. The level of fragmentation per species compared to (a) the amount of vertebrate in the diet (%), (b) body mass, and (c) the number of references from the primary literature. Colours indicate different carnivorous mammal Orders. For certain species of larger body sizes and levels of carnivory, there is some increased level of fragmentation in the species' range. The number of references, as a proxy for how well-known a species' ecology is, shows the reverse, with no trend of higher references correlating with level of fragmentation.

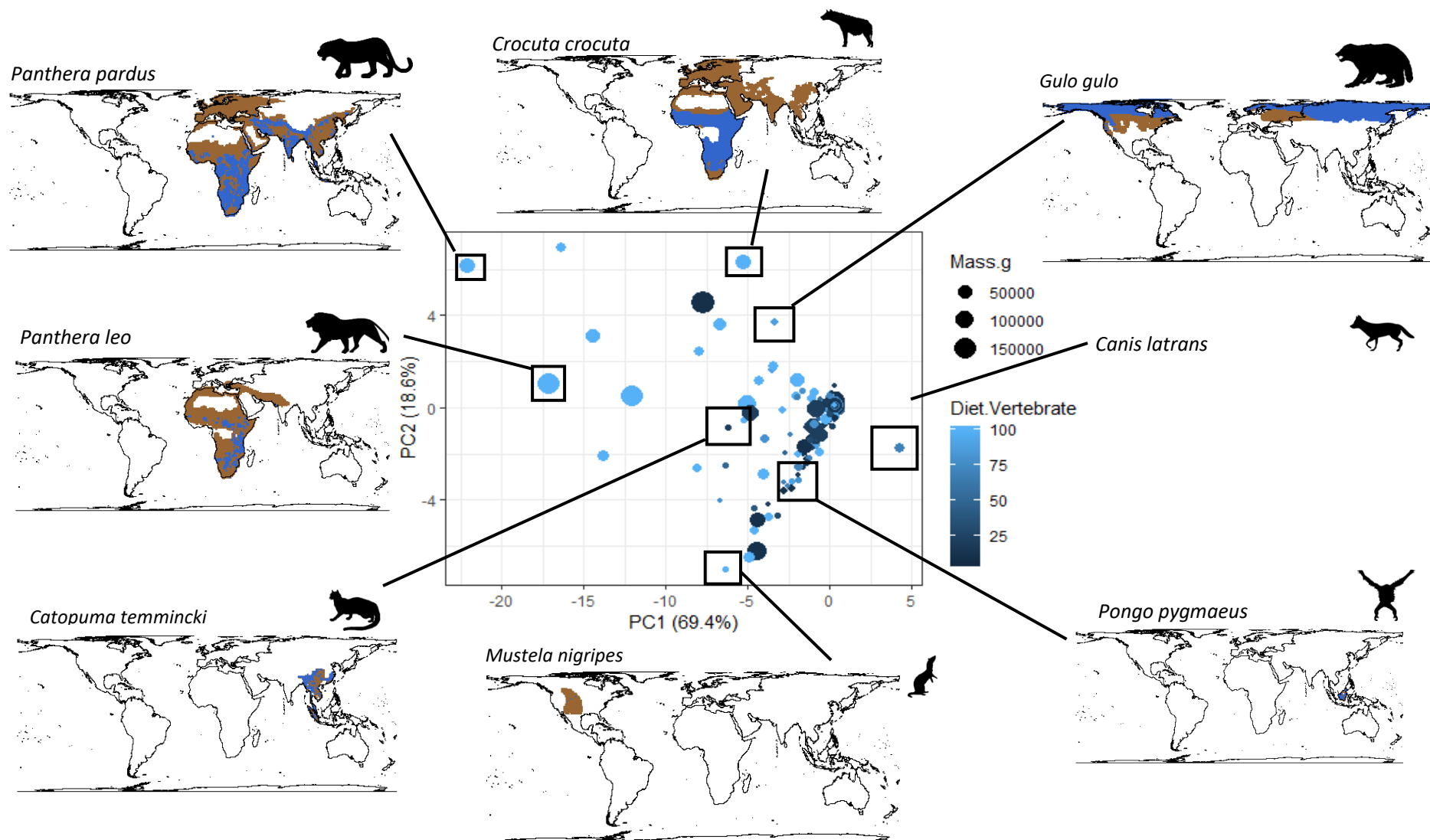


FIGURE A2.13 | Different forms of geographic range fragmentation across carnivorous mammals. Location of species in Euclidean space (middle) following a PCA of three variables, describing geographic range shapes. Species were chosen to demonstrate extremes from the present-natural to current.

9.1.2 | Tables

TABLE A2.1. Bayesian model fits. Hierarchical partitioning of constructed BBPMMs and selection by average DIC score from models run on each of the 100 sampled mammalian phylogenies for all species ($n = 1\,081$ species). Each model was run with 200 000 iterations, a burn-in period of 10 000, and thinning interval of 100. Models are ordered in ascending order of support, with the lowest DIC score indicating the best-supported model. PRD = proportional range difference; VC = Vertebrate consumption (%); BM = $\text{Log}_{10}(\text{body mass, g})$; P = phylogenetic covariance matrix, as a random effect.

Model	DIC
PRD ~ VC * BM + (1 P)	113353.7
PRD ~ VC + BM + (1 P)	113354.1
PRD ~ VC + (1 P)	113354.6
PRD ~ BM + (1 P)	113355.6

TABLE A2.2 | Best-supported Bayesian model coefficients. Effects of scaled $\text{log}_{10}(\text{body mass})$ and scaled vertebrate consumption (%) on the proportional difference of carnivorous mammals ($n = 1081$), between the present-natural and current. Average estimates (log-odds ratios), lower and upper 95% credible intervals (CI) were calculated from the best-supported model run on 100 sampled mammalian phylogenetic trees. VC = Vertebrate consumption (%); BM = $\text{log}_{10}(\text{body mass})$.

Variable	Estimate	Lower CI (95%)	Upper CI (95%)
(Intercept)	-18.18	-33.35	-3.59
BM	9.11	6.58	11.97
VC	1.27	-0.77	3.34
BM:VC	1.52	0.13	2.97
Phylogeny	175.95	68.79	366.53
Residuals	90.73	62.51	128.16

TABLE A2.3 | Bayesian model fits with only systematically reviewed species. Effects Hierarchical partitioning of constructed BBPMMs and selection by average DIC score from models run on each of the 100 sampled mammalian phylogenies using only the systematically review species ($n = 555$ species). Each model was run with 200 000 iterations, a burn-in period of 10 000, and thinning interval of 100. Models are ordered in ascending order of support, with the lowest DIC score indicating the best-supported model. PRD = proportional range difference; VC = Vertebrate consumption (%); BM = $\text{log}_{10}(\text{body mass, g})$; P = phylogenetic covariance matrix, as a random effect.

Model	DIC
PRD ~ VC * BM + (1 P)	111986.2
PRD ~ VC + BM + (1 P)	111986.2
PRD ~ BM + (1 P)	111986.6
PRD ~ VC + (1 P)	111987.9

TABLE A2.4 | Best-supported Bayesian model coefficients with only systematically reviewed species For systematically reviewed species, the average log-odds ratio estimates, upper and lower 95% credible intervals from the best-supported model, run with 100 sampled mammalian phylogenetic trees. Both predictor variables were scaled, with single unit increases states in the methods. VC = Vertebrate consumption (%); BM = $\log_{10}$ (body mass, g).

Variable	Estimate	Lower CI (95%)	Upper CI (95%)
(Intercept)	-13.36	-30.2	2.77
BM	7.97	5.24	11.06
VC	0.99	-1.48	3.49
BM:VC	1.42	-0.13	2.99
Phylogeny	217.88	91.40	440.04
Residuals	61.30	39.89	89.67

TABLE A2.5 | Principal components analysis output for changes in species geographic ranges from the current to present-natural. Proportion of variance and cumulative proportion of variation explained by three principal components returned. The first two PCs explain 88% of the variation. The influence of three variables on PCs is shown.

	PC1	PC2	PC3
Standard deviation (σ)	1.44	0.75	0.60
Proportion of variance	0.70	0.19	0.12
Cumulative proportion	0.70	0.88	1.00
Influence of variables			
Range change	0.58	-0.55	0.60
Core Area Index change	0.54	0.81	0.22
Number of clumps change	-0.61	0.20	0.77

9.2 | Chapter 3

9.2.1 | Figures

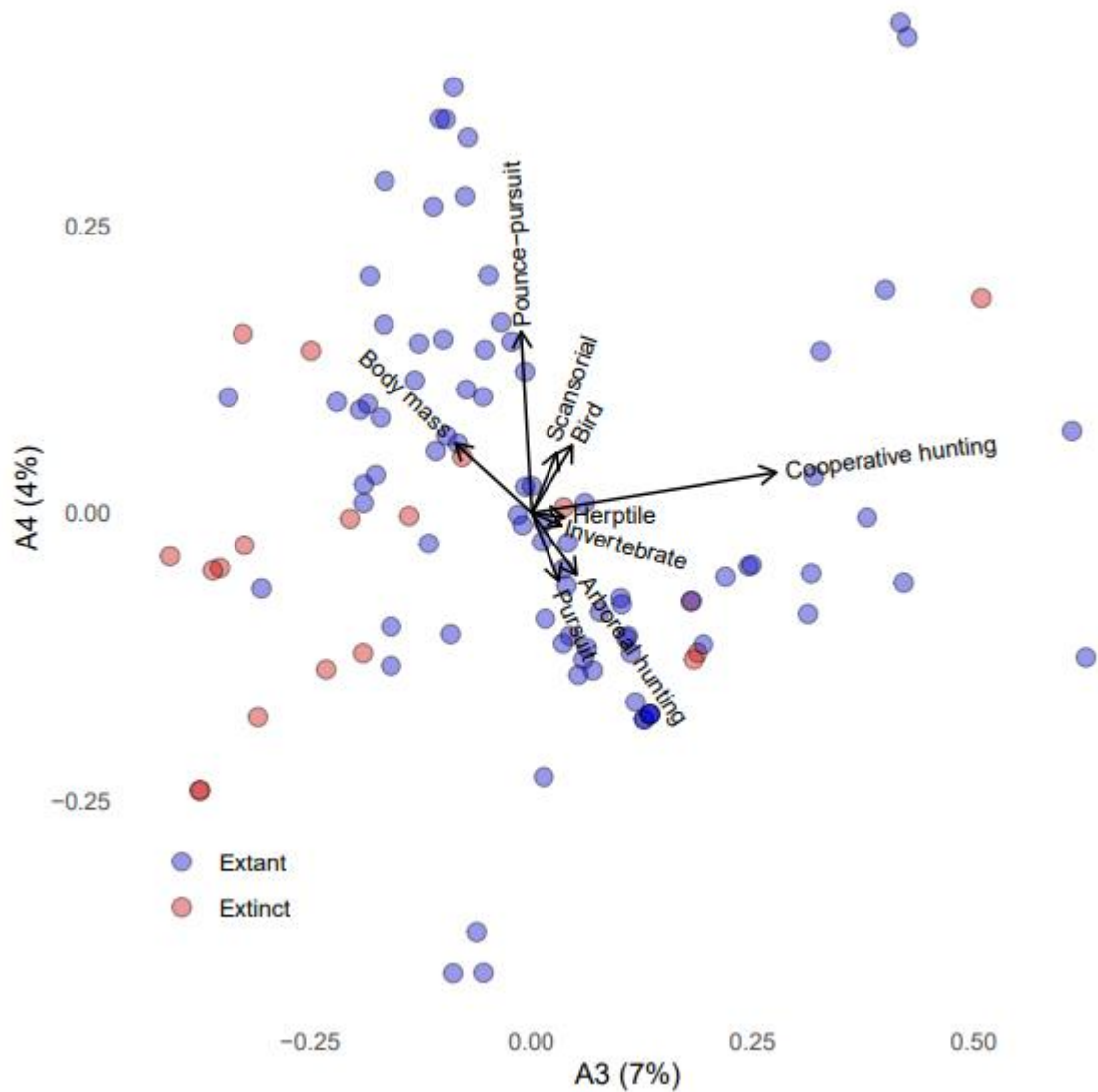


FIGURE A3.1 | Additional axes of global hypercarnivore functional trait space. Third and fourth axes of global functional trait space showing pair-wise dissimilarity of all extinct (red) and extant (blue) species (equally transparent and sized points) based on their functional traits. Arrows show individual traits scaled by their contribution to the structure of the global functional trait space.

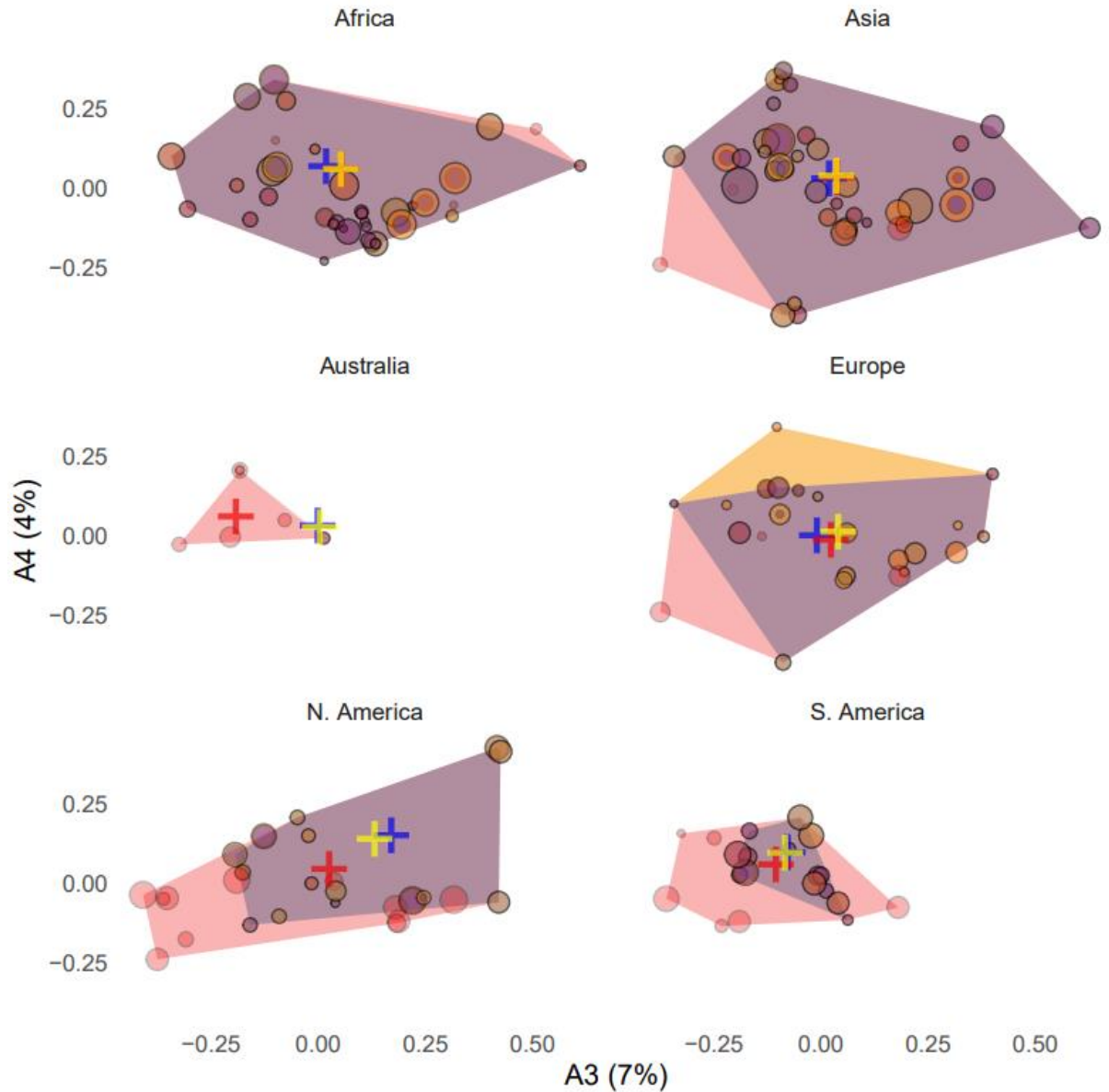


FIGURE A3.2 | Additional axes of continental hypercarnivore trait spaces. Third and fourth axes of continental assemblages with points scaled by species' past (red), current (blue), and recolonized (yellow) geographic ranges sizes (GR). Polygons represent the functional richness of the past (red), current (yellow), and recolonised (yellow) assemblages. Crosses indicate the geographic range-weighted assemblage centroids representing functional dispersion.

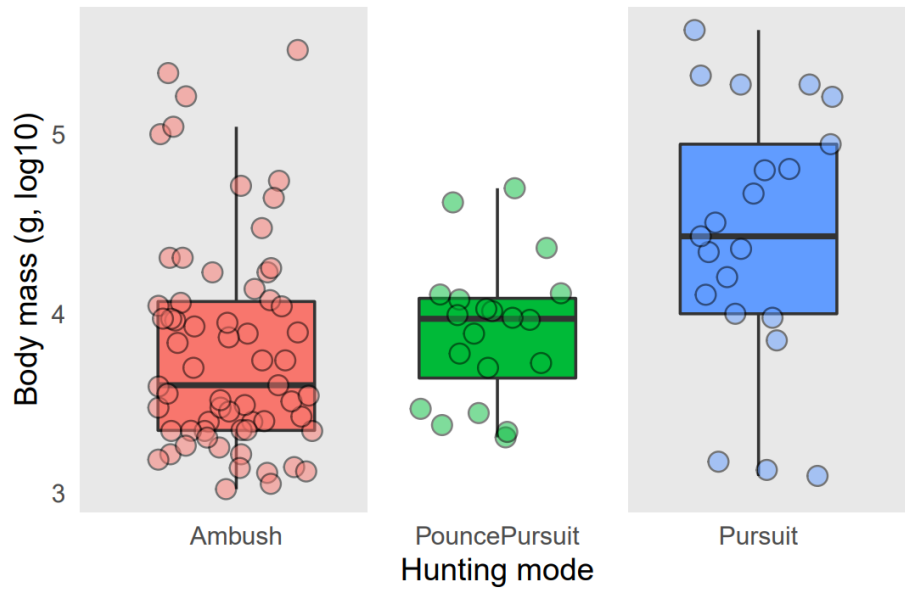


FIGURE A3.3 | Body mass (log₁₀) of hypercarnivores with different hunting modes. Boxplots indicate median, upper and lower quartiles. Whiskers indicate non-outlier minimum and maximum values. Outliers are points that are 1.5 times the interquartile range away from the upper or lower quartile.

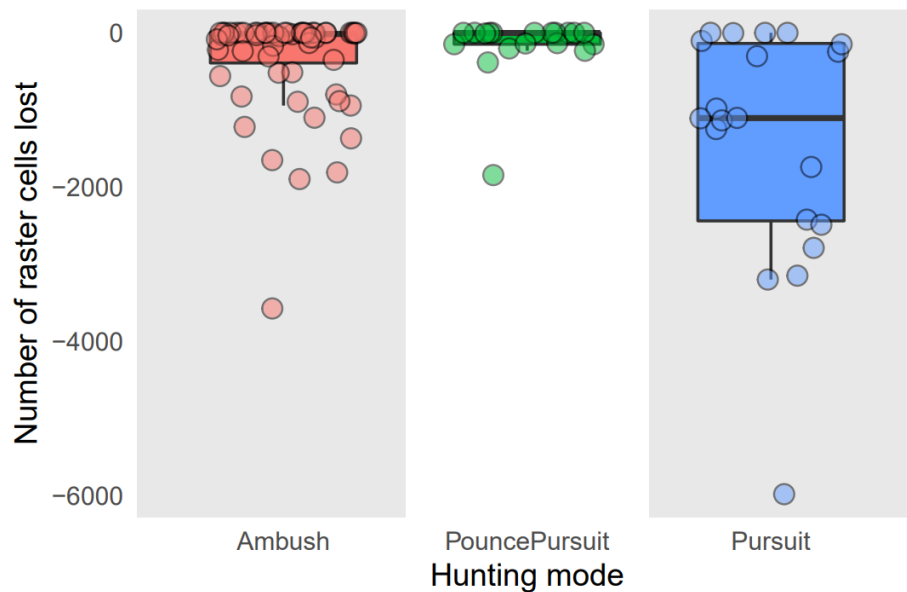


FIGURE A3.4 | Geographic range loss by hypercarnivores with different hunting modes. The number of raster cells lost between the present-natural and current-day range maps from Phylacine v1.2, for hypercarnivores (circles) of different hunting modes. Boxplots indicate median, upper and lower quartiles. Whiskers indicate non-outlier minimum and maximum values. Outliers are points that are 1.5 times the interquartile range away from the upper or lower quartile.

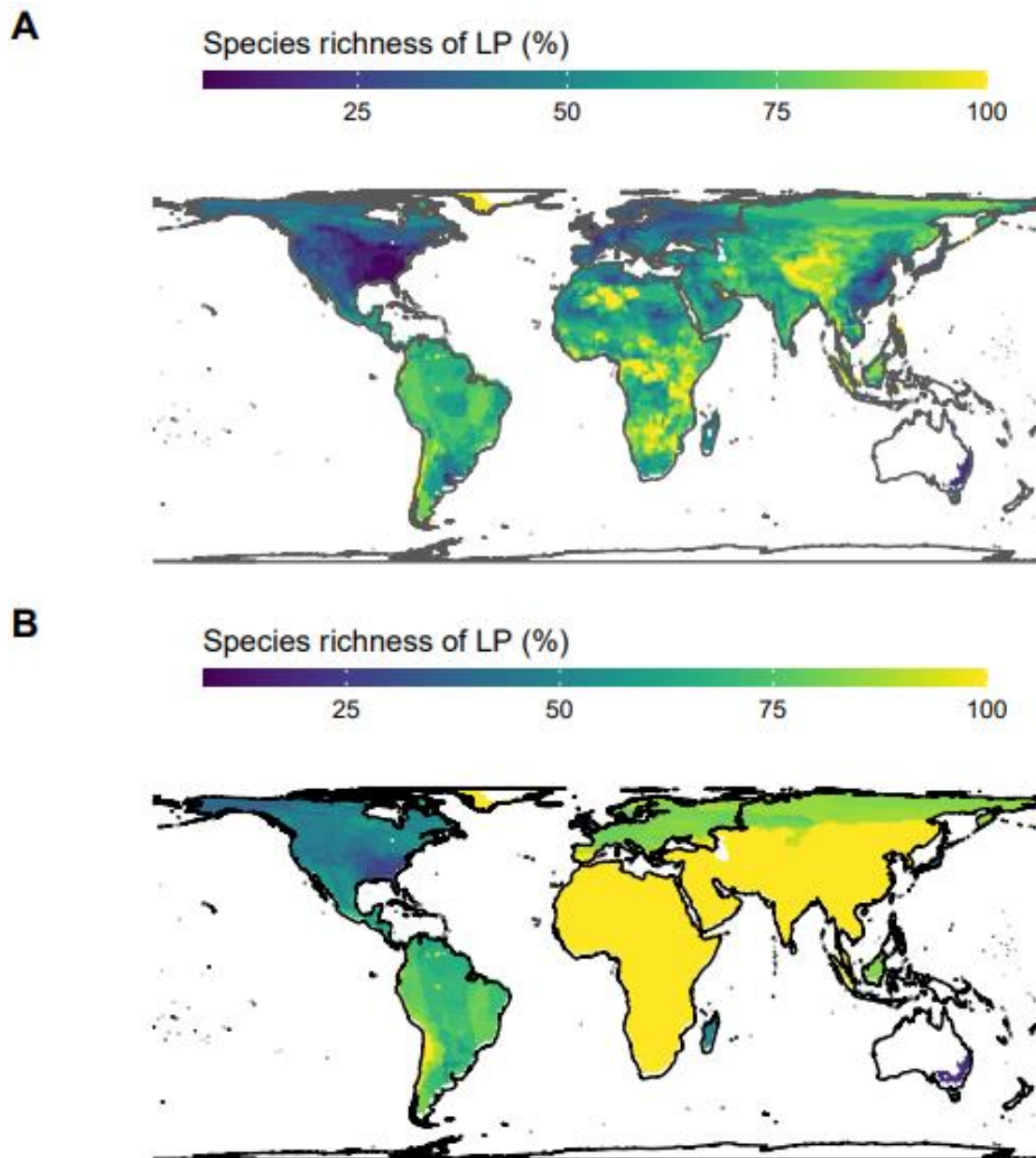


FIGURE A3.5 | Species richness of (a) current-day assemblages, and (b) assemblages following recolonisations, relative to LP species richness. Brighter colours indicate a greater restoration of species richness to LP levels. Maps are shown on a Behrmann equal-area projection with an overlaying shapefile of the world's continents.

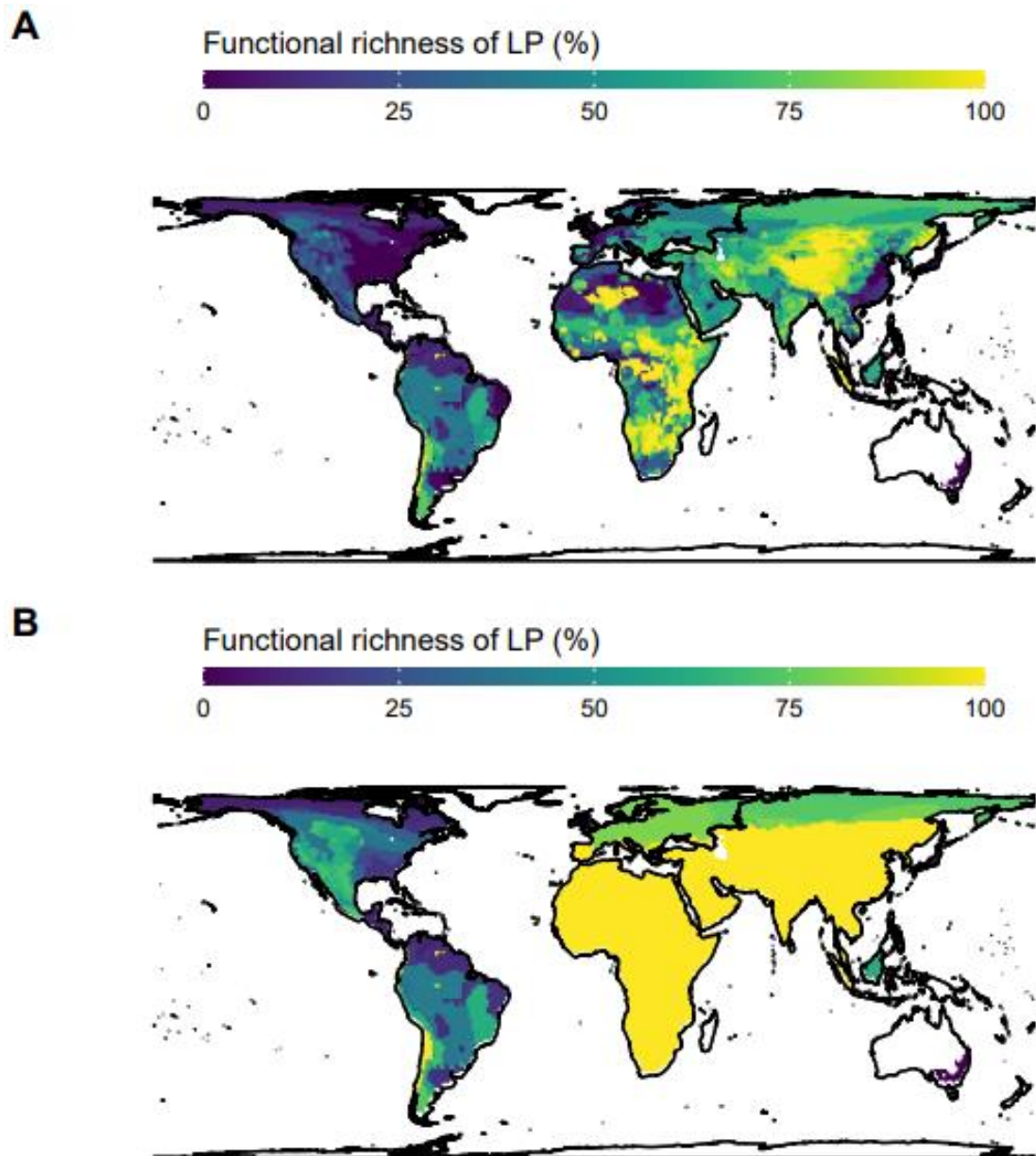


FIGURE A3.6 | Functional richness of (a) current-day assemblages, and (b) assemblages following recolonisations, relative to LP functional richness. Brighter colours indicate a greater restoration of functional richness to LP levels. Maps are shown on a Behrmann equal-area projection with an overlaying shapefile of the world's continents.

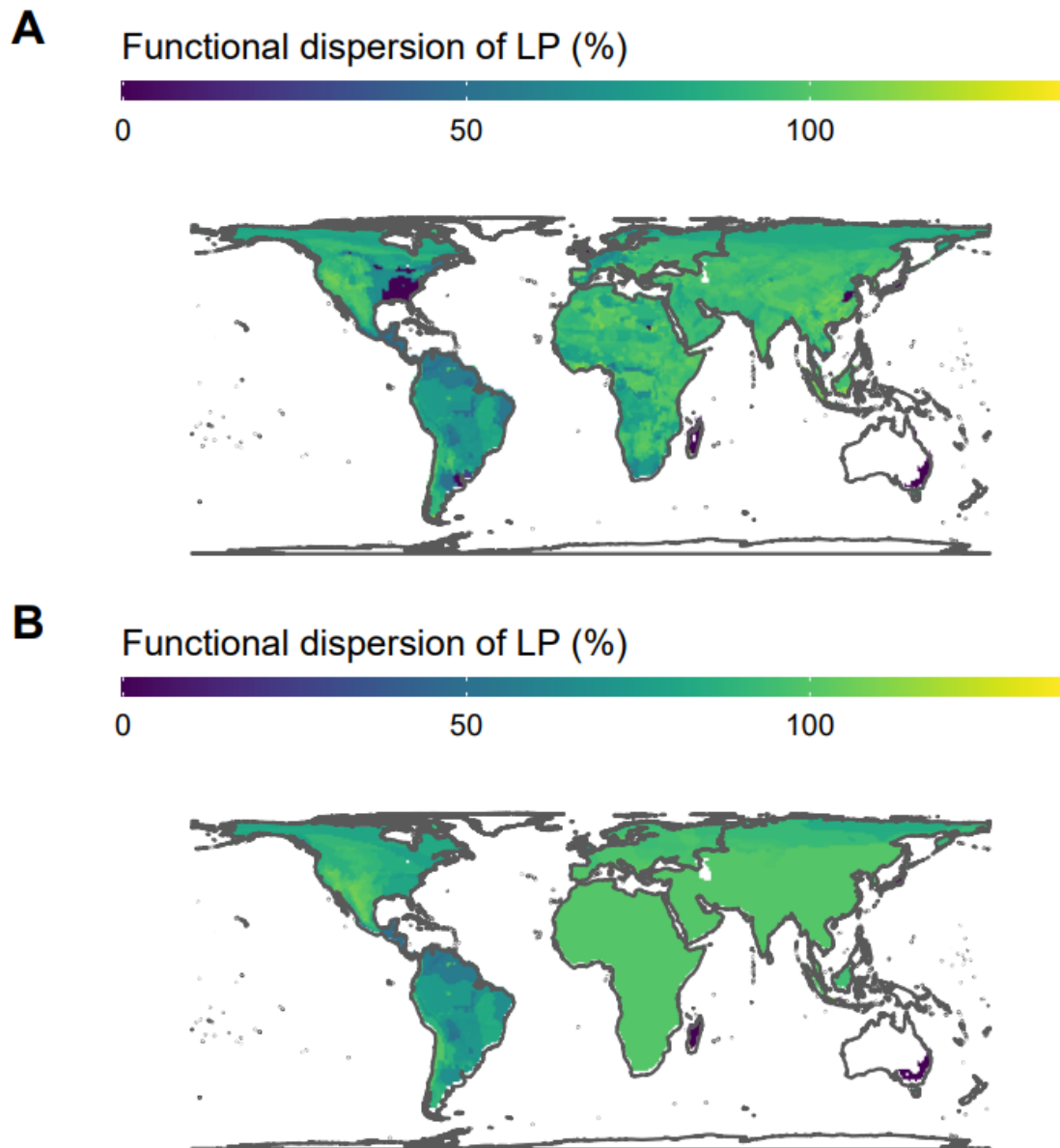


FIGURE A3.7 | Functional dispersion of (a) current-day assemblages, and (b) assemblages following recolonisations, relative to LP functional dispersion. Brighter colours indicate a greater restoration of functional dispersion to LP levels. Maps are shown on a Behrmann equal-area projection with an overlaying shapefile of the world's continents.

9.2.2 | Tables

TABLE A3.1 | Notable differences between IUCN range maps Version 2016-3 and Version 2021-3. Species with notable differences in geographic ranges between these two versions were included here. Any ranges with seemingly random and very minor discrepancies that likely resulted as a methodological artefact were deemed compatible.

Species	Total range difference (+/-%)	Explanation	Notes
<i>Canis aureus</i>	-58.5%	Taxonomic split and range expansion	The decline is attributed to the loss of the former geographic range of golden jackals in Africa. However, these populations still exist but are now recognised as a distinct species (African wolf; <i>Canis lupaster</i>). Golden jackals have also increased in Europe and across India in well-documented range expansion events.
<i>Canis lupus</i>	+4.5%	Range expansion and loss	Range expansion widely across Europe and in India. Range loss in Southern Greenland and Western US. Also range expansion in Northern Greenland.
<i>Panthera onca</i>	+4%	Range expansion and loss	Mixture of range expansion and range loss in 2021 ranges compared to 2016. Overall net increase.
<i>Panthera uncia</i>	+11.4%	Range expansion	Apparent range expansion particularly in Northern geographic range.

9.3 | Chapter 4

9.3.1 | Figures

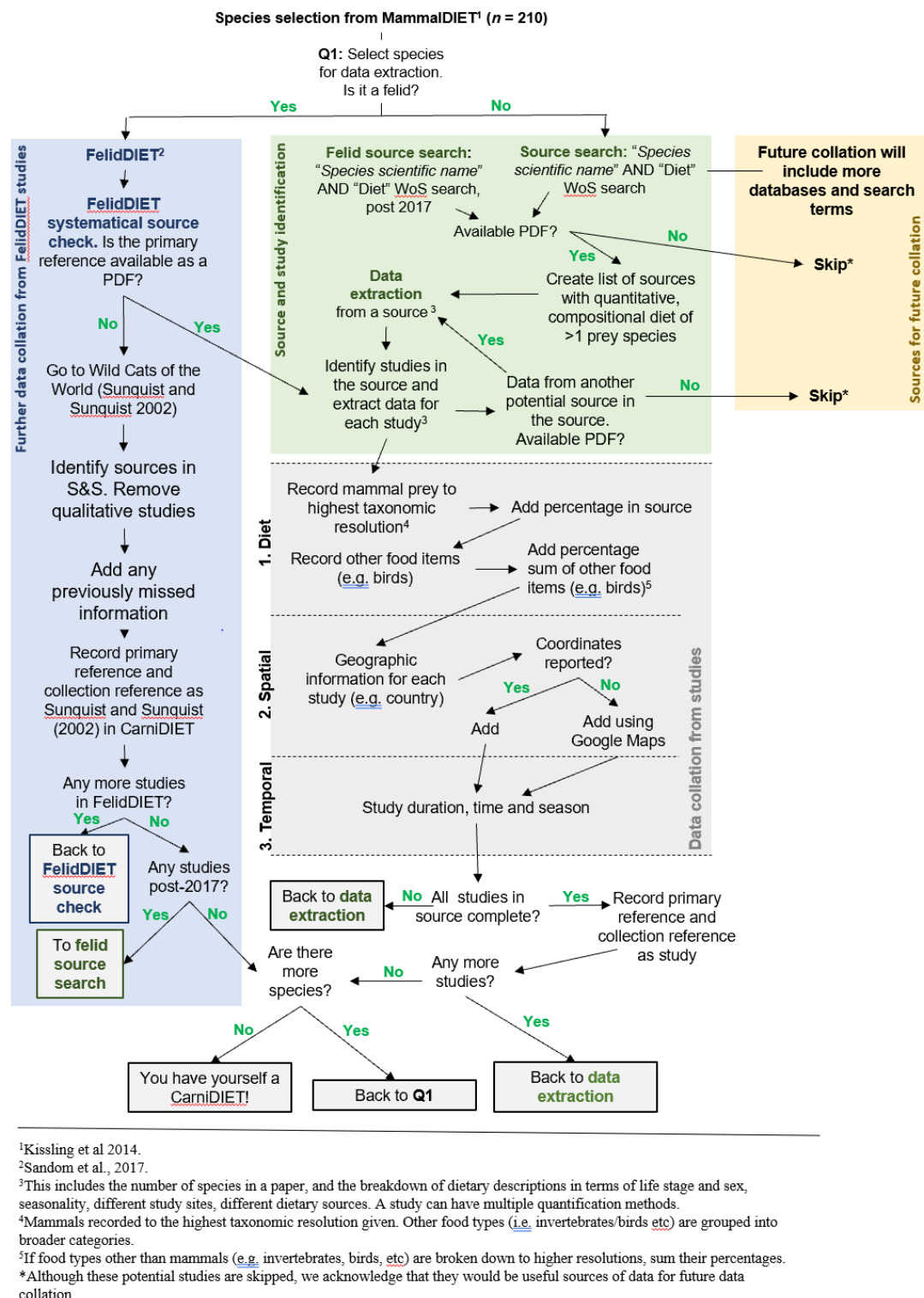


FIGURE A4.1 | Flow diagram for the construction of CarniDIET 1.0 from species identification, source search, identification, to data extraction from individual diet studies within sources. Grey boxes refer to databases. Orange boxes refer to potentially useful sources of data for future collation efforts that were excluded from CarniDIET 1.0.

Conceptual diagram of CarniDIET's structure

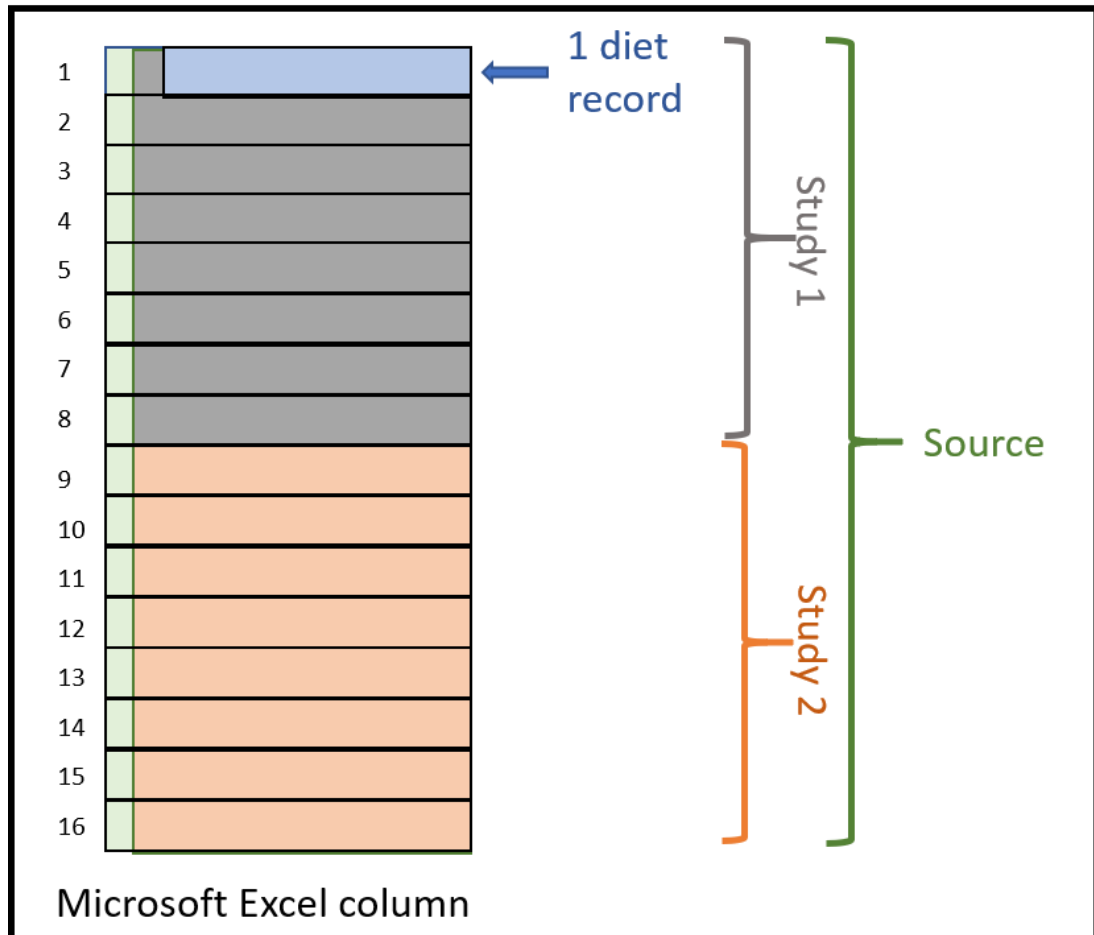


FIGURE A4.2 | Terminology in CarniDIET. Conceptual diagram providing an overview of CarniDIET structure and key terminology using an example of a source which has two studies (e.g. a species of mammal-consumer across a single year in two difference study sites) that consist of 8 diet records per study and 16 total diet records for the source.

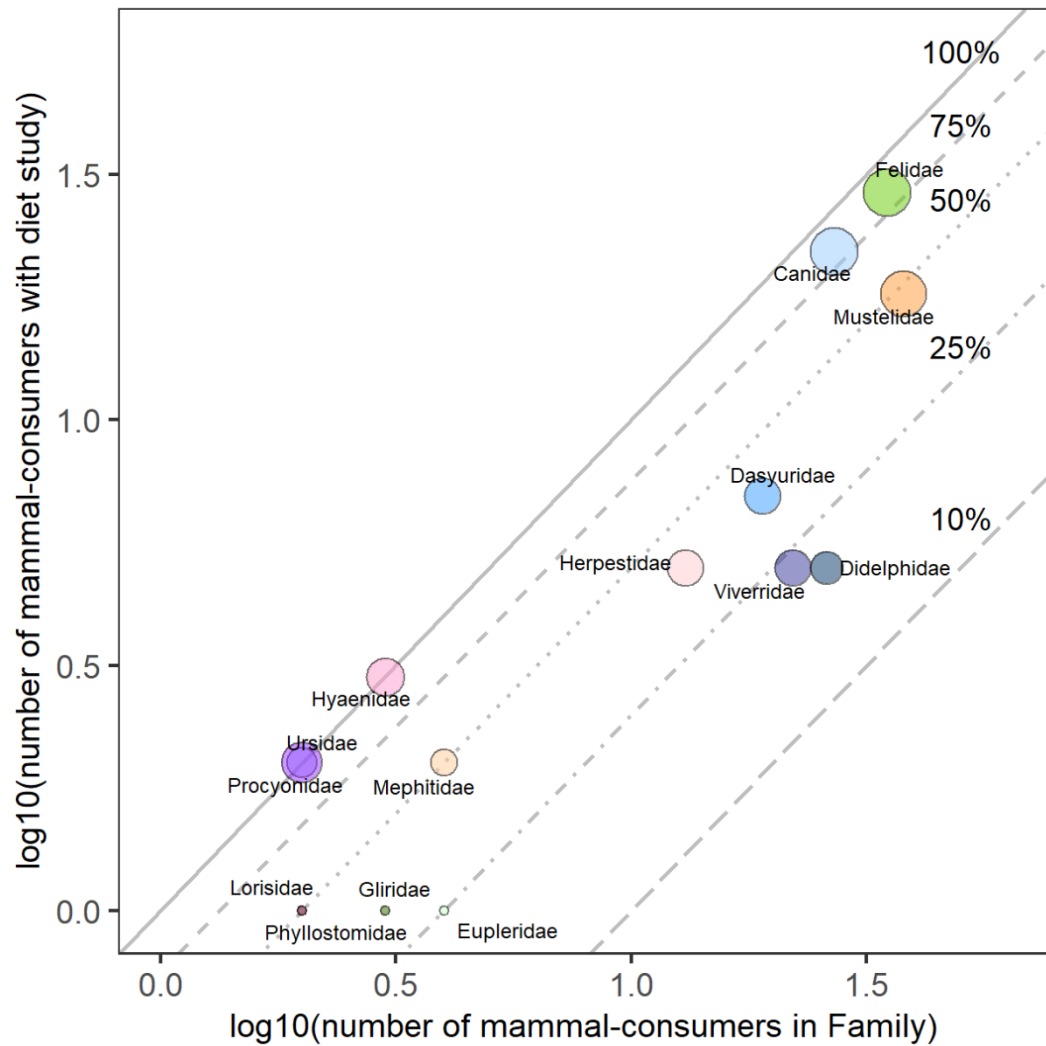


FIGURE A4.3 | Taxonomic coverage of species with studies in CarniDIET. The number of mammal-consumers with one, or more, diet study in CarniDIET against the number of described mammal-consumers within each of 15 families with at least one mammal-consumer study. Diagonal lines indicate the percentage representation (shown for 100%, 75%, 50%, 25%, and 10%). Size of equally-transparent points reflect the number of sources for that family (log₁₀-scale).

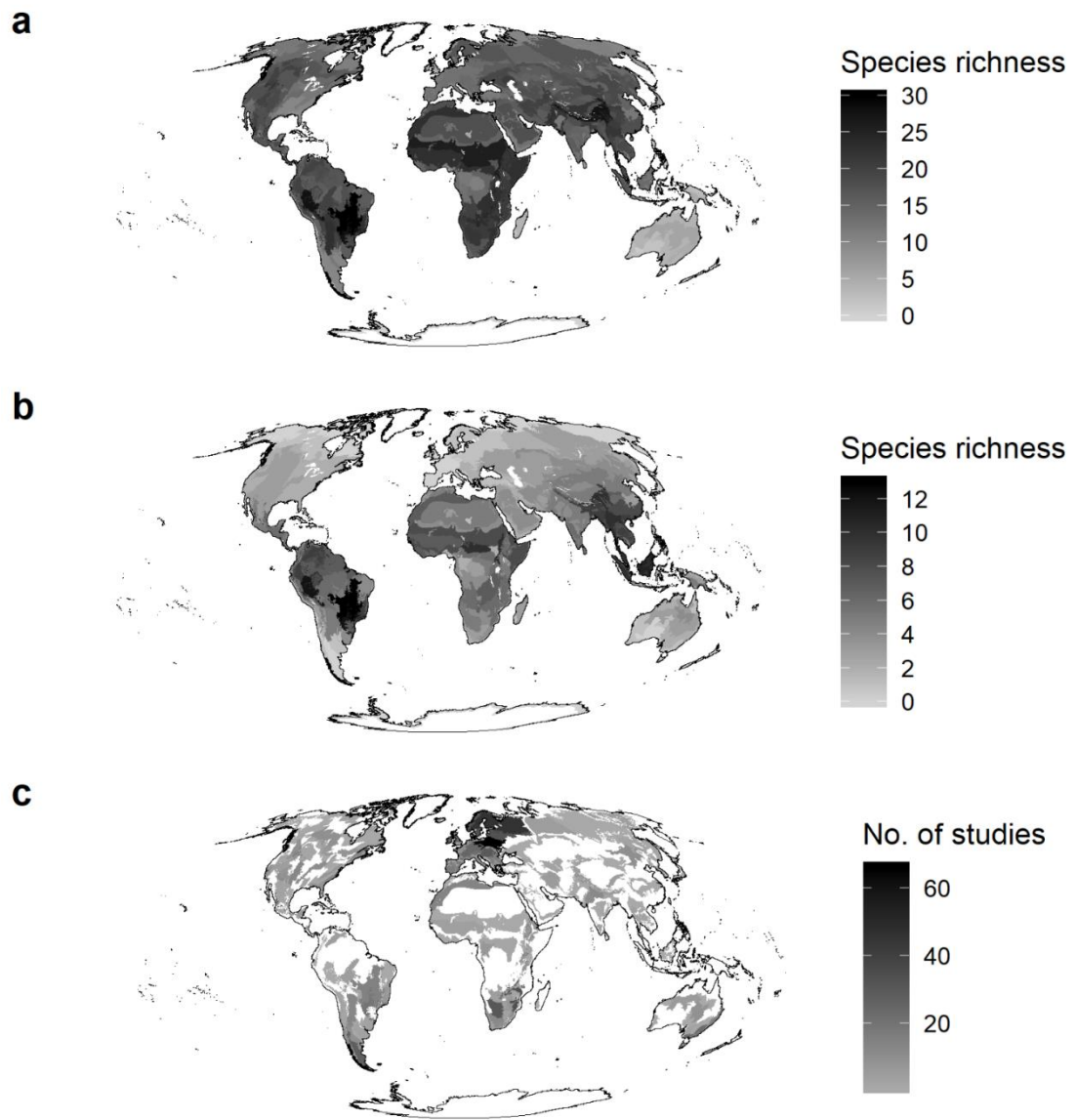


FIGURE A4.4 | Distribution of mammal-consumer species and diet studies by ecoregion. (a) Total species richness of all potential mammal consumers (n = 210). (b) Species richness of mammal-consumers that do not have a single diet study (n = 107). (c) Number of mammal-consumer diet studies in CarniDIET.

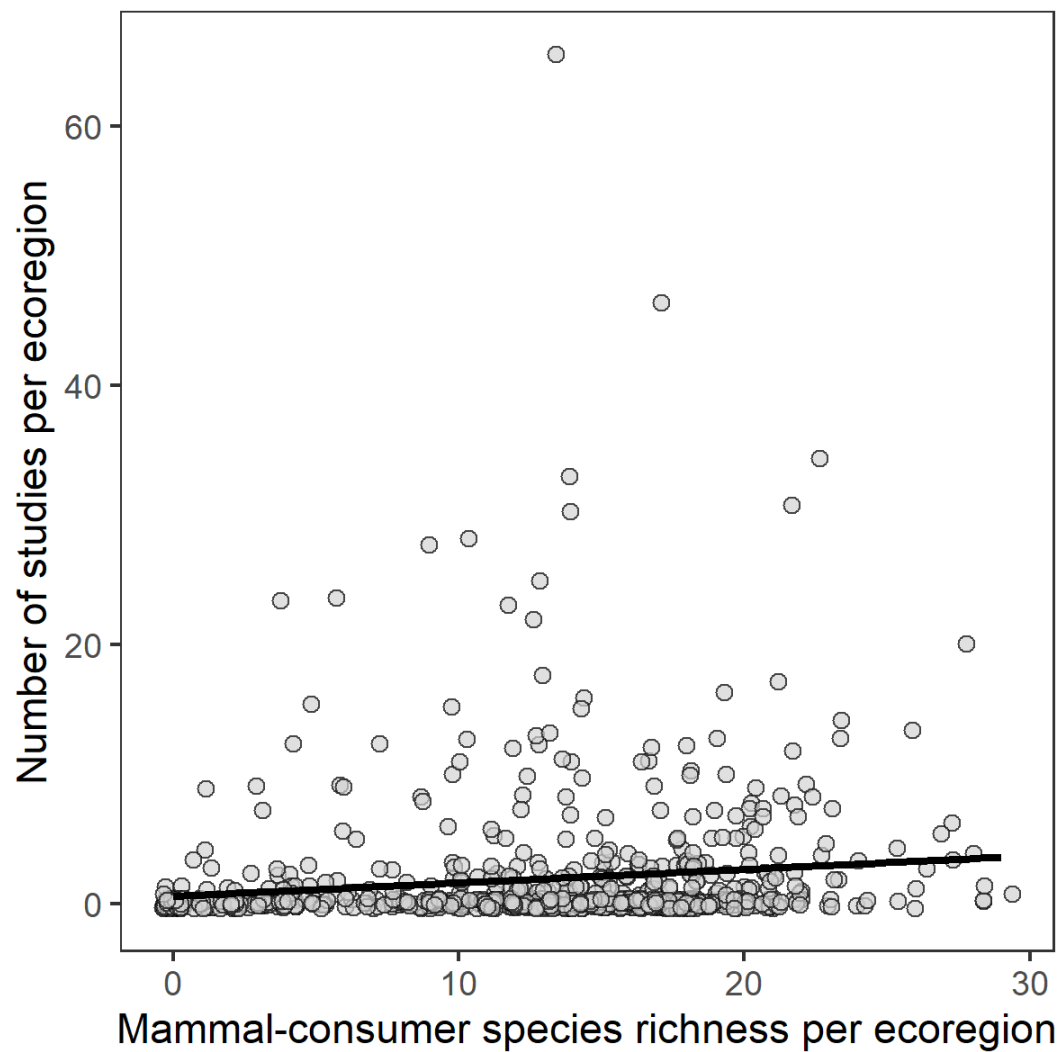


FIGURE A4.5 | Relationship between mammal-consumer species richness and the number of diet studies completed per ecoregion (Pearson's correlation coefficient = 0.15). Points (equal-transparency and jittered for clarity) represent ecoregions, excluding "Rock & Ice" and "Lake" (n = 825).

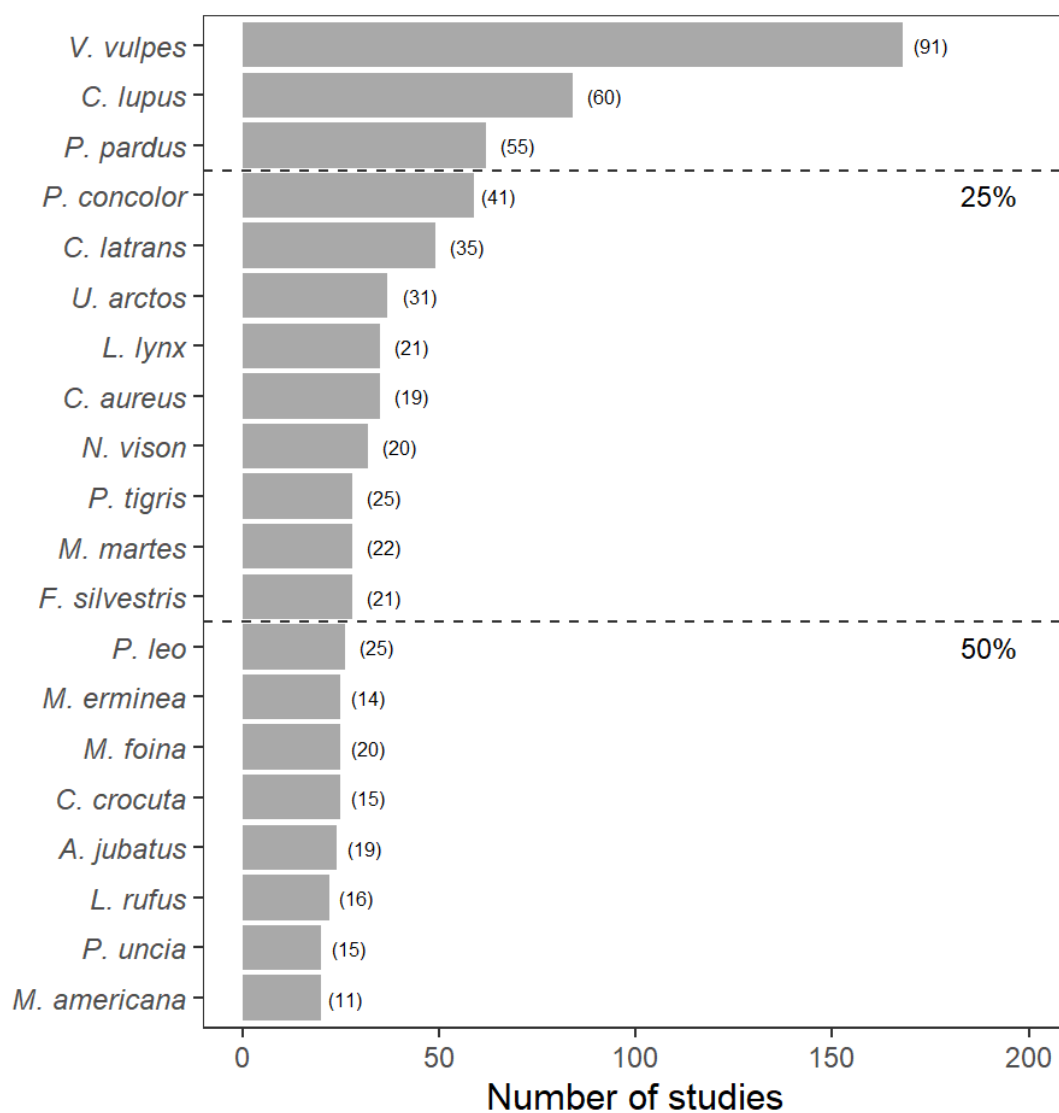


FIGURE A4.6 | The top-20 most studied species in CarniDIET. Species are shown in descending order from first (red fox, *Vulpes vulpes*) to twentieth (American marten, *Martes americana*). Bars indicate the number of studies per mammal consumer, and numbers in parentheses indicates the number of sources form which studies were extracted.

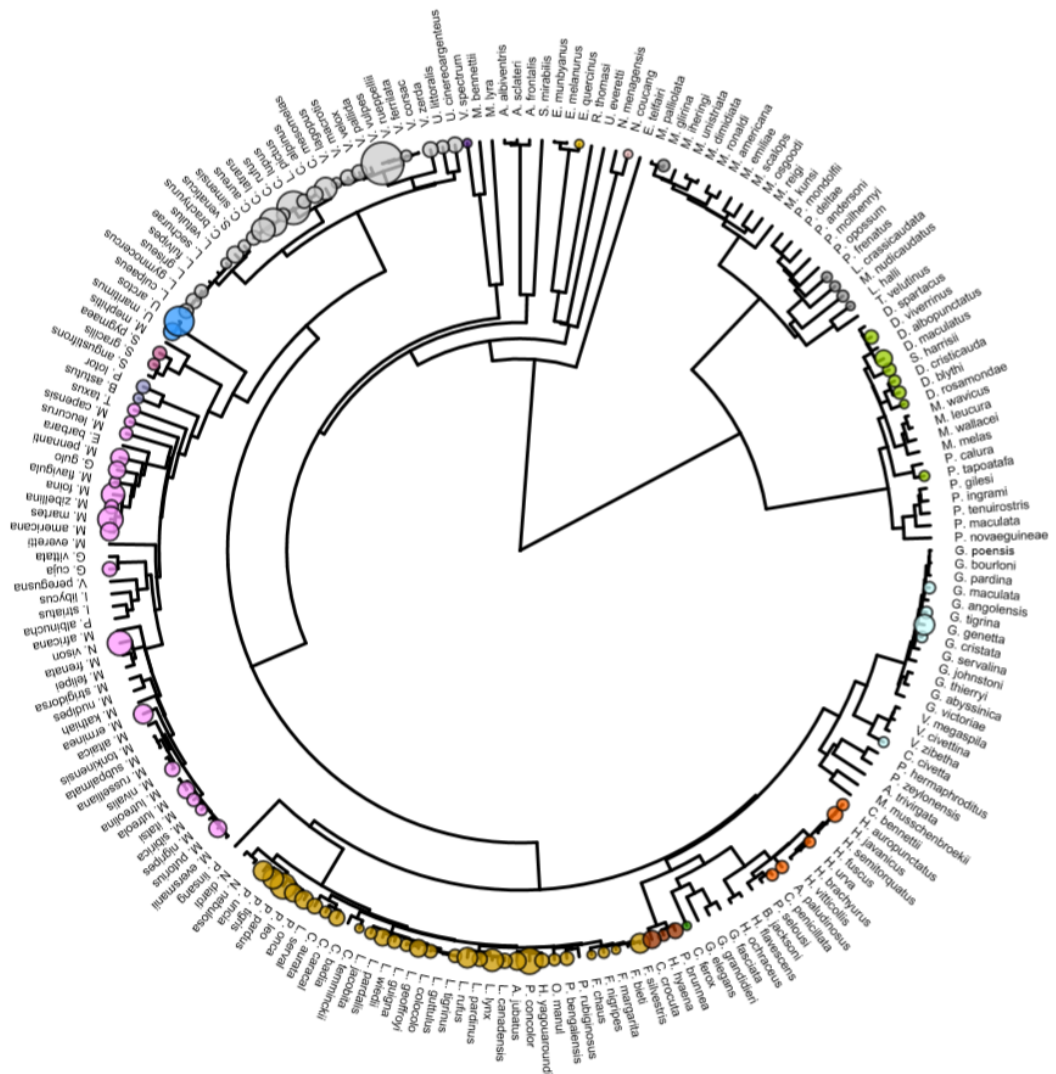


FIGURE A4.7 | Phylogeny (Faurby *et al.*, 2018) of 210 potential mammal-consumers in CarniDIET from 23 families. Tree tips with circles (equal transparency; colours indicate different families) indicate species with dietary studies (size of circle indicates the number of studies) and those without indicate absence of dietary studies.

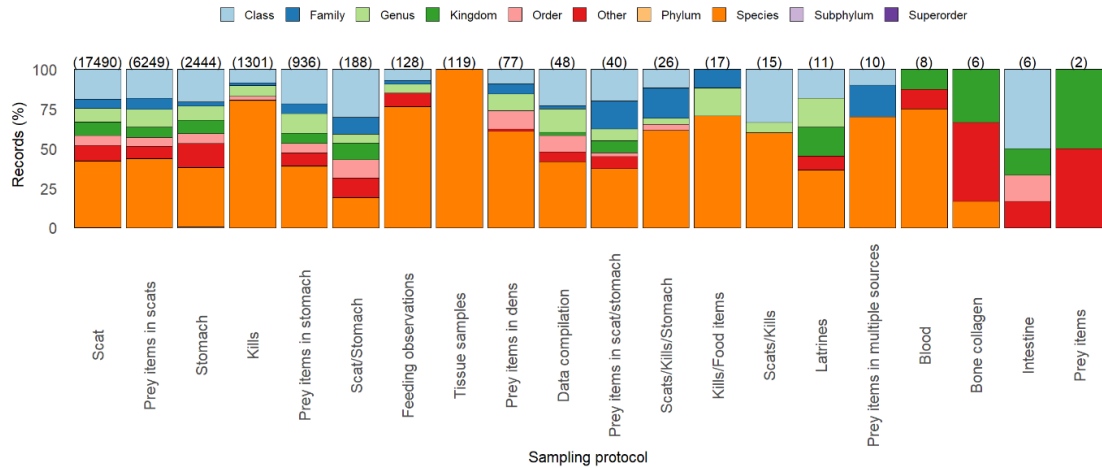


FIGURE A4.8 | Same as Figure 2b, with all records. We include all combinations of sampling protocols and taxonomic resolutions. From left to right, sampling protocols are listed from those with the most to the least diet record.

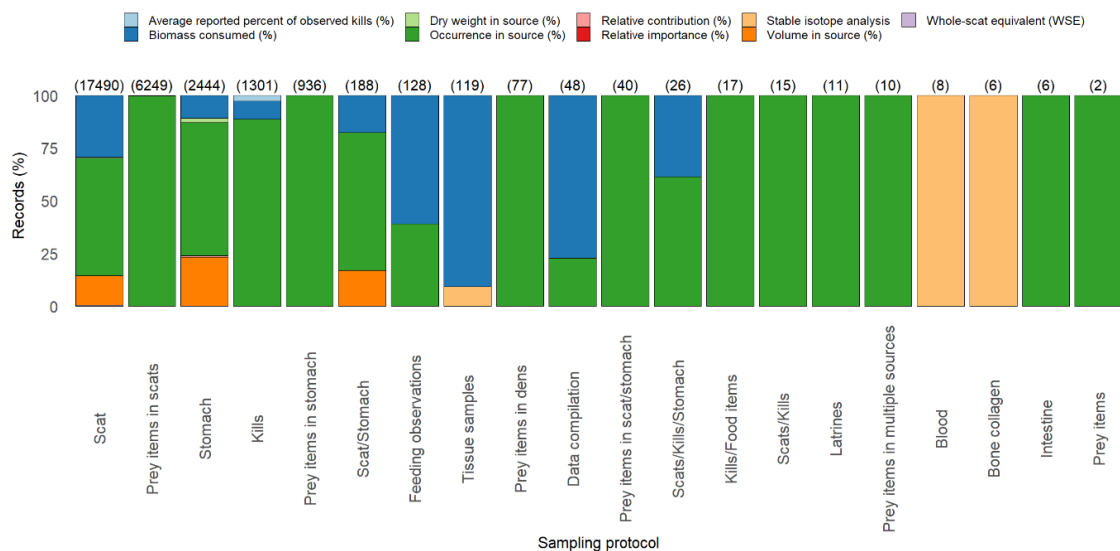


FIGURE A4.9 | Same as Figure 2c, with all records. We include all combinations of sampling protocols and quantification methods. From left to right, sampling protocols are listed from those with the most to the least diet record.

9.3.2 | Tables

TABLE A4.1 | Data availability for mammalian taxonomic families with at least one mammal-consumer. The representation of each taxonomic family (Rep (%)) is given as a percentage of the number of species in that family with at least one dietary study relative to the number of possible mammal-consumer species in that family.

Order	Family	Total species	Species with >1 diet study	Rep (%)	Number of potential WoS Sources	Number of WoS Sources with diet data	Potential WoS sources with diet data (%)	Median number of sources for species in family	Maximum number of sources for species in family
Afrosoricida	Tenrecidae	1	0	0	1	0	0	0	0
Carnivora	Canidae	27	22	81	1074	269	25	5	91
	Eupleridae	4	1	25	12	1	8	1	1
	Felidae	35	29	83	892	233	26	6	53
	Herpestidae	13	4	31	36	14	39	3.5	6
	Hyaenidae	3	3	100	78	23	29	8	15
	Mephitidae	4	2	50	14	3	21	1.5	2
	Mustelidae	38	18	47	524	123	23	6	22
	Prionodontidae	1	0	0	0	0	0	0	0
	Procyonidae	2	2	100	26	5	19	2.5	4
	Ursidae	2	2	100	327	41	13	20.5	31
	Viverridae	22	5	23	48	17	35	2	12
Chiroptera	Megadermatidae	1	0	0	3	0	0	0	0
	Phyllostomidae	2	1	50	2	1	50	1	1
Dasyuromorphia	Dasyuridae	19	7	37	48	17	35	2	10
Didelphimorphia	Didelphidae	26	5	19	31	8	26	2	2
Eulipotyphla	Erinaceidae	3	0	0	0	0	0	0	0
	Soricidae	1	0	0	0	0	0	0	0
Primates	Lorisidae	2	1	50	6	1	17	1	1
	Pitheciidae	2	0	0	6	0	0	0	0
Rodentia	Cricetidae	1	0	0	0	0	0	0	0
	Gliridae	3	1	33	9	1	11	1	1
Scandentia	Tupaiaidae	1	0	0	0	0	0	0	0

TABLE A4.2 | Data availability for mammalian taxonomic genera with at least one mammal-consumer. The representation of each genus (Rep (%)) is given as a percentage of the number of species in that genus with at least one dietary study relative to the number of possible mammal-consumer species in that genus. *Genera with more sources with diet data than potential WoS sources occur because of sources for which we went back to primary sources presenting the original data that did not appear in the original WoS searches.

Order	Family	Genus	Total species	Species with >1 diet study	Rep (%)	Number of potential WoS Sources	Number of sources with diet data	Potential WoS sources with diet data (%)	Median number of sources for species in family	Maximum number of sources for species in family
Afrosoricida	Tenrecidae	Echinops	1	0	0	1	0	0	0	0
Carnivora	Canidae	Canis	6	6	100	472	128	27	15	60
	Canidae	Chrysocyon	1	1	100	41	11	27	11	11
	Canidae	Cuon	1	1	100	26	12	46	12	12
	Canidae	Lycalopex	6	4	66.7	31	13	42	4.5	6
	Canidae	Lycaon	1	1	100	36	10	28	10	10
	Canidae	Speothos	1	1	100	10	2	20	2	2
	Canidae	Urocyon	2	2	100	23	6	26	3	4
	Canidae	Vulpes	9	6	66.7	435	104	24	3.5	91
	Eupleridae	Cryptoprocta	1	1	100	9	1	11	1	1
	Eupleridae	Galidia	1	0	0	1	0	0	0	0
	Eupleridae	Galidictis	2	0	0	2	0	0	0	0
	Felidae	Acinonyx	1	1	100	60	19	33	20	20
	Felidae	Caracal	2	2	100	10	10	120*	6	10
	Felidae	Catopuma	2	1	50	3	1	33	1	1
	Felidae	Felis	5	4	80	86	18	21	2	15
	Felidae	Herpailurus	1	1	100	2	6	300*	6	6
	Felidae	Leopardus	8	7	87.5	62	24	39	5	11
	Felidae	Leptailurus	1	1	100	3	3	100	3	3
	Felidae	Lynx	4	4	100	159	41	26	10	19
	Felidae	Neofelis	2	0	0	6	0	0	0	0
	Felidae	Otocolobus	1	1	100	1	2	200*	2	2

Felidae	Panthera	5	5	100	347	107	31	22	53
Felidae	Prionailurus	2	1	50	33	10	30	10	10
Felidae	Puma	1	1	100	120	38	32	38	38
Herpestidae	Atilax	1	1	100	7	4	57	4	4
Herpestidae	Bdeogale	1	0	0	0	0	0	0	0
Herpestidae	Cynictis	1	1	100	6	3	50	3	3
Herpestidae	Herpestes	9	2	22	23	8	35	4	6
Herpestidae	Paracynictis	1	0	0	0	0	0	0	0
Hyaenidae	Crocuta	1	1	100	65	15	23	15	15
Hyaenidae	Hyaena	1	1	100	7	3	43	3	3
Hyaenidae	Parahyaena	1	1	100	6	8	133*	8	8
Mephitidae	Mephitis	1	0	0	10	0	0	0	0
Mephitidae	Spilogale	3	2	66.7	4	3	75	1.5	2
Mustelidae	Eira	1	0	0	3	0	0	0	0
Mustelidae	Galictis	2	1	50	13	6	46	6	6
Mustelidae	Gulo	1	1	100	20	7	35	7	7
Mustelidae	Ichonyx	2	0	0	1	0	0	0	0
Mustelidae	Martes	6	6	100	185	61	33	10	22
Mustelidae	Meles	1	1	100	3	1	33	1	1
Mustelidae	Mellivora	1	1	100	2	1	50	1	1
Mustelidae	Melogale	1	0	0	0	0	0	0	0
Mustelidae	Mustela	19	6	31.6	203	31	15	5.5	14
Mustelidae	Neovison	1	1	100	87	20	23	20	20
Mustelidae	Poecilogale	1	0	0	0	0	0	0	0
Mustelidae	Taxidea	1	1	100	6	2	33	2	2
Mustelidae	Vormela	1	0	0	1	0	0	0	0
Prionodontidae	Prionodon	1	0	0	0	0	0	0	0
Procyonidae	Bassariscus	1	1	100	3	1	33	1	1
Procyonidae	Procyon	1	1	100	23	4	17	4	4
Ursidae	Ursus	2	2	100	327	41	13	20.5	31

	Viverridae	Arctogalidia	1	0	0	0	0	0	0	0
	Viverridae	Civettictis	1	1	100	4	1	25	1	1
	Viverridae	Cynogale	1	0	0	0	0	0	0	0
	Viverridae	Genetta	13	4	30.8	37	16	43	2	12
	Viverridae	Macrogalidia	1	0	0	0	0	0	0	0
	Viverridae	Paradoxurus	2	0	0	6	0	0	0	0
	Viverridae	Viverra	3	0	0	1	0	0	0	0
Chiroptera	Megadermatidae	Megaderma	1	0	0	3	0	0	0	0
	Phyllostomidae	Mimon	1	0	0	1	0	0	0	0
	Phyllostomidae	Vampyrum	1	1	100	1	1	100	1	1
Dasyuromorphia	Dasyuridae	Dasycercus	2	2	100	4	3	75	2	2
	Dasyuridae	Dasykaluta	1	1	100	1	1	100	1	1
	Dasyuridae	Dasyurus	4	2	50	28	11	39	6	10
	Dasyuridae	Myoictis	4	0	0	0	0	0	0	0
	Dasyuridae	Phascogale	2	1	50	3	1	33	1	1
	Dasyuridae	Planigale	5	0	0	3	0	0	0	0
	Dasyuridae	Sarcophilus	1	1	100	9	3	33	3	3
Didelphimorphia	Didelphidae	Lestodelphys	1	1	100	3	1	33	1	1
	Didelphidae	Lutreolina	1	1	100	7	2	29	2	2
	Didelphidae	Metachirus	1	1	100	9	2	22	2	2
	Didelphidae	Monodelphis	16	1	6.3	3	1	33	1	1
	Didelphidae	Philander	6	1	16.7	7	2	29	2	2
	Didelphidae	Thylamys	1	0	0	2	0	0	0	0
Eulipotyphla	Erinaceidae	Atelerix	3	0	0	0	0	0	0	0
	Soricidae	Sorex	1	0	0	0	0	0	0	0
Primates	Lorisidae	Nycticebus	2	1	50	6	1	17	1	1
	Pitheciidae	Pithecia	2	0	0	6	0	0	0	0
Rodentia	Cricetidae	Rheomys	1	0	0	0	0	0	0	0
	Gliridae	Eliomys	3	1	33.3	9	1	11	1	1

Scandentia	Tupaiidae	Urogale	1	0	0	0	0	0	0	0
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9.4 | Chapter 5

9.4.1 | Figures

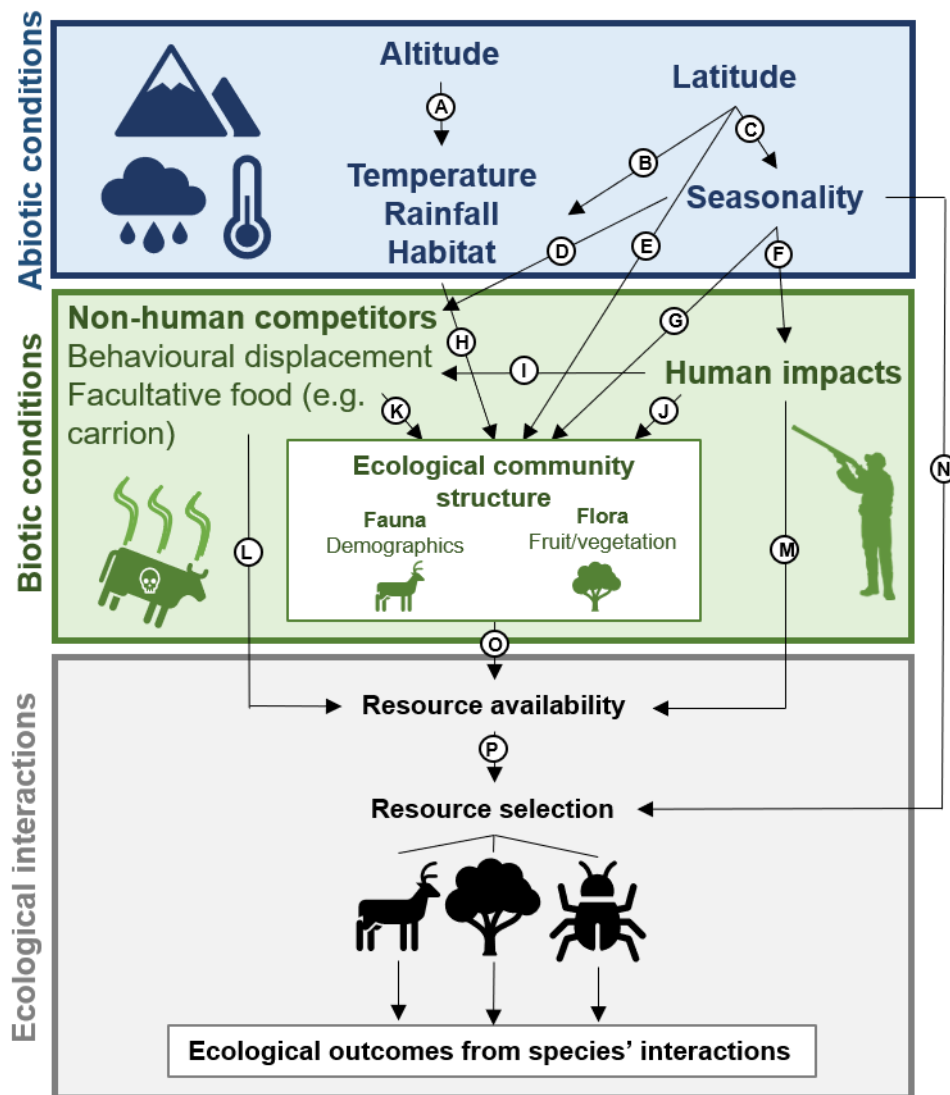


FIGURE A5.1 | Connections between abiotic and biotic conditions that can influence local environmental context, and in turn carnivore resource availability and resource selection. The conceptual figure presents a hypothetical overview of the potential links between abiotic and biotic conditions that mediate the formation of a species' diet. As such, we acknowledge there will be further conditions, and links, that can further influence resource availability and selection. The conceptual figure was built upon a previously constructed conceptual model on diet selection as an ecosystem process by (Ellis *et al.*, 1976). Justification for each link are as follows: (A) altitude influences local climatic conditions; (B) latitude influences local climatic conditions; (C) seasonal climate changes with latitude; (D) the effects of non-human competitors can change depending on their resource selection (e.g. different amount of carrion provisioning across seasons); (E) ecological community structures changes with latitude depending on species present; (F) human impacts can vary across seasons (e.g. hunting seasons); (G) seasonal effects can modify ecological community structures (e.g. migration); (H) habitat structures, as determined by local climatic conditions can influence ecological community assembly; (I) human impacts can modify the effects of apex predators (e.g. persecution); (J) widespread human impacts can modify the structure of ecological communities through localized extinctions and/or introductions; (K) the presence of larger

carnivores can influence the behavior and population dynamics of larger prey species that can mediate vegetation communities; (L) competitors can influence resource availability to smaller predators through facultative provisioning of carrion; (M) humans can influence resource availability through facultative food provisioning; (N) resource selection can change seasonally depending on species' macronutrient requirements (e.g. hibernating species); (O) the structure of the ecological community largely determines the availability of resources to carnivores; (P) resource selection is largely determined by available resources.

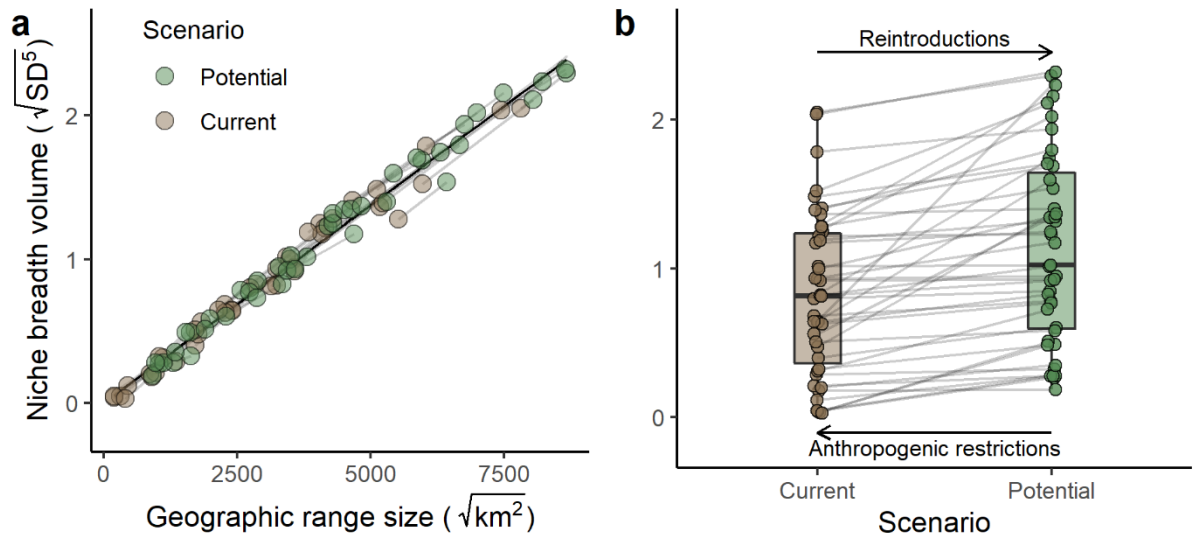


FIGURE A5.2 | Current and potential geographic range size and ecological niche breadths of reintroduction candidates. (a) The relationship between geographic range size and environmental niche breadth of species in their current (brown points) and potential (green points) geographic ranges. The linear regression model prediction is shown (black line) with standard error (grey ribbon). (b) Difference in species' environmental niche breadths between their current and potential geographic ranges, with grey lines indicating the same species. From left to right indicates the maximum increase in environmental niche breadth volume following a species reintroduction to its full potential range, and from right to left indicates the decrease in ecological niche breadth following anthropogenic range restriction.

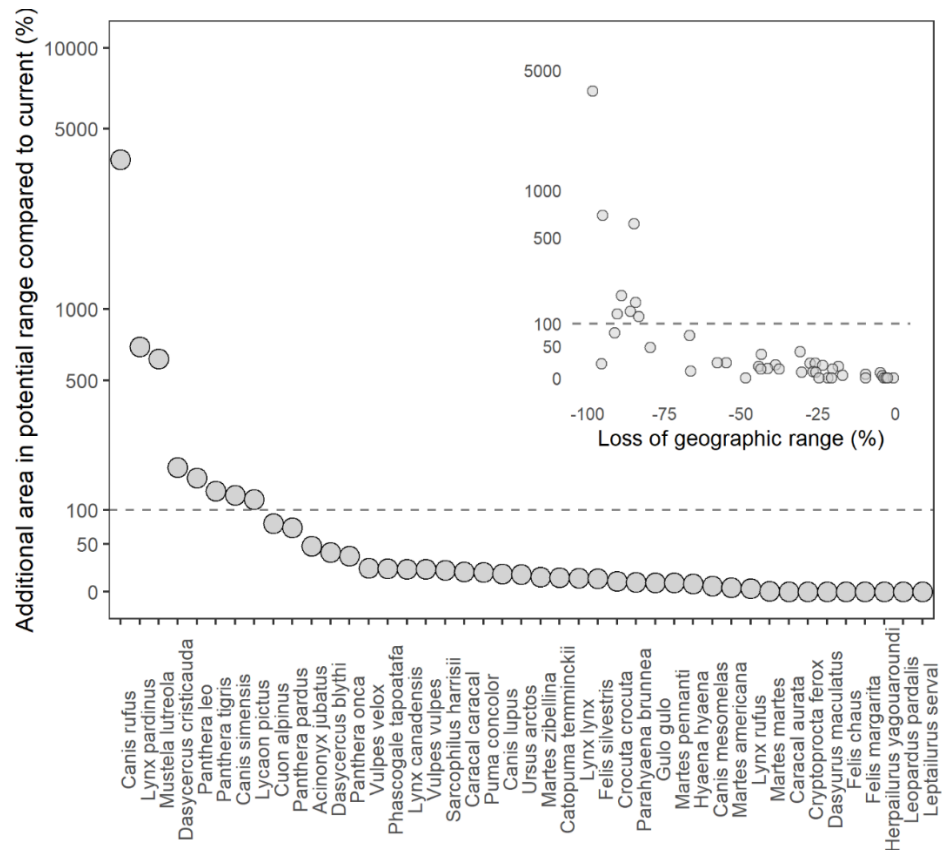


FIGURE A5.3 | The additional area (%) in species' potential geographic ranges, relative to their current ranges, with environmental contexts represented by those of diet when environmental context is described with five variables. Species are ranked from left to right by those with the highest relative additional area in potential range compared to their current range. The inset plot shows the relationship between additional area (%) and loss of geographic range (%). Species with >100% additional area represented (dashed line) in their potential range have a greater geographic scope for reintroductions than for in-situ conservation within their current range.

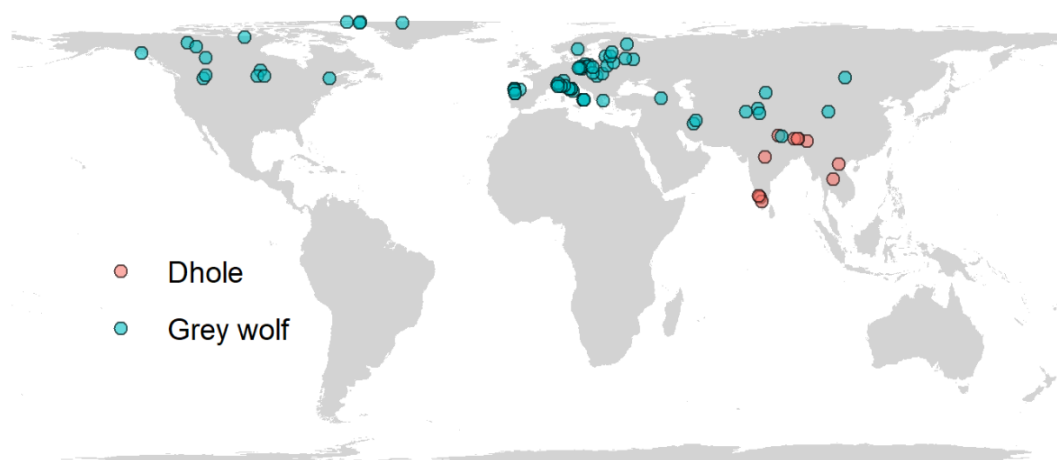
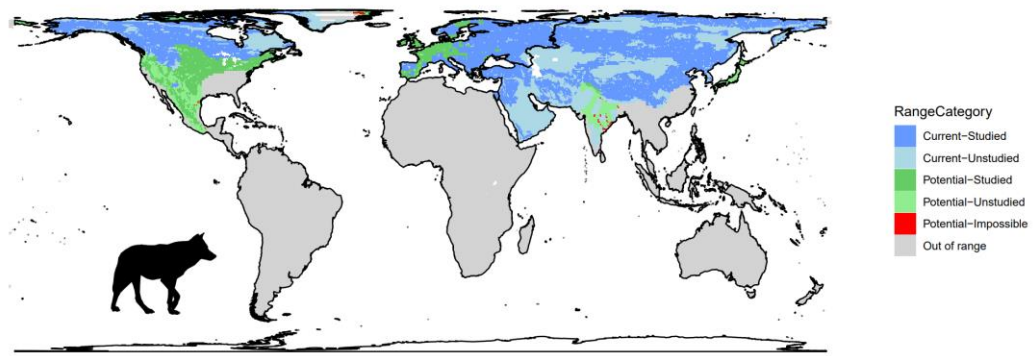


FIGURE A5.4 | The location of diet studies for grey wolves (*Canis lupus*; blue) and dholes (*Cuon alpinus*; red). Points are equal transparency to show overlapping diet study locations.

a



b

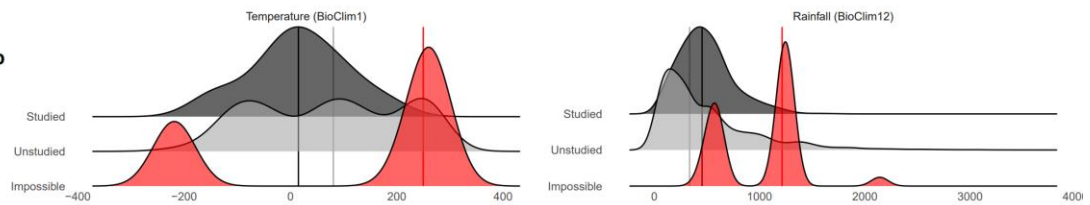
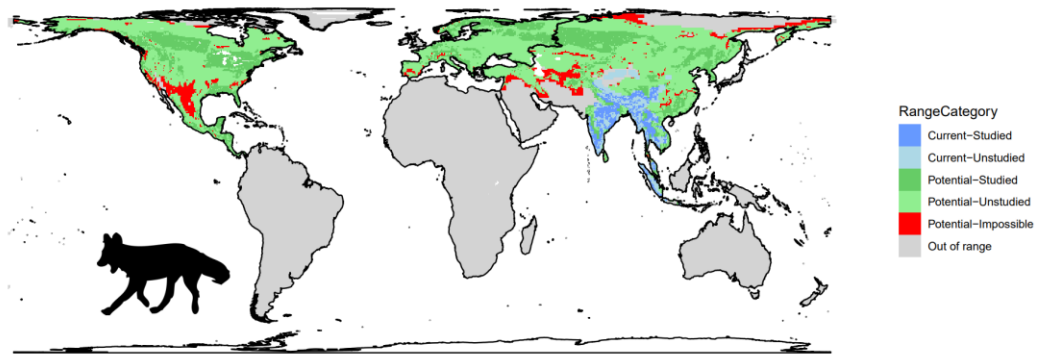


FIGURE A5.5 | Representation of temperature and rainfall geographic range of grey wolves by their diet studies. (a) The potential (light grey) and current (dark grey) geographic ranges of grey wolves and the areas (cells) with environments that fall within studied hypervolumes when environmental niche breadths were constructed using two (light blue) to five dimensions (dark blue). (b) For the five-dimensional environmental niche breadth hypervolume, the density of areas which differ in standard deviations from the mean of each centered and scaled variable are shown within the current, potential, and studied hypervolumes. Median value of areas are shown for the current and potential geographic range and areas represented by diet studies (i.e. “Studied”) are shown with vertical lines.

a



b

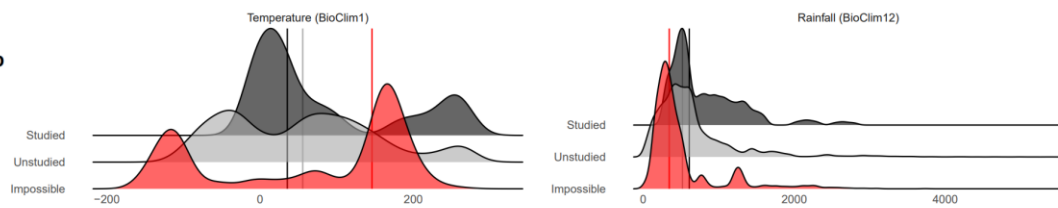


FIGURE A5.6 | Representation of temperature and rainfall geographic range of dholes by their diet studies. (a) The potential (light grey) and current (dark grey) geographic ranges of grey wolves and the areas (cells) with environments that fall within studied hypervolumes when environmental niche breadths were constructed using two (light blue) to five dimensions (dark blue). (b) For the five-dimensional environmental niche breadth hypervolume, the density of areas which differ in standard deviations from the mean of each centered and scaled variable are shown within the current, potential, and studied hypervolumes. Median value of areas are shown for the current and potential geographic range and areas represented by diet studies (i.e. “Studied”) are shown with vertical lines.

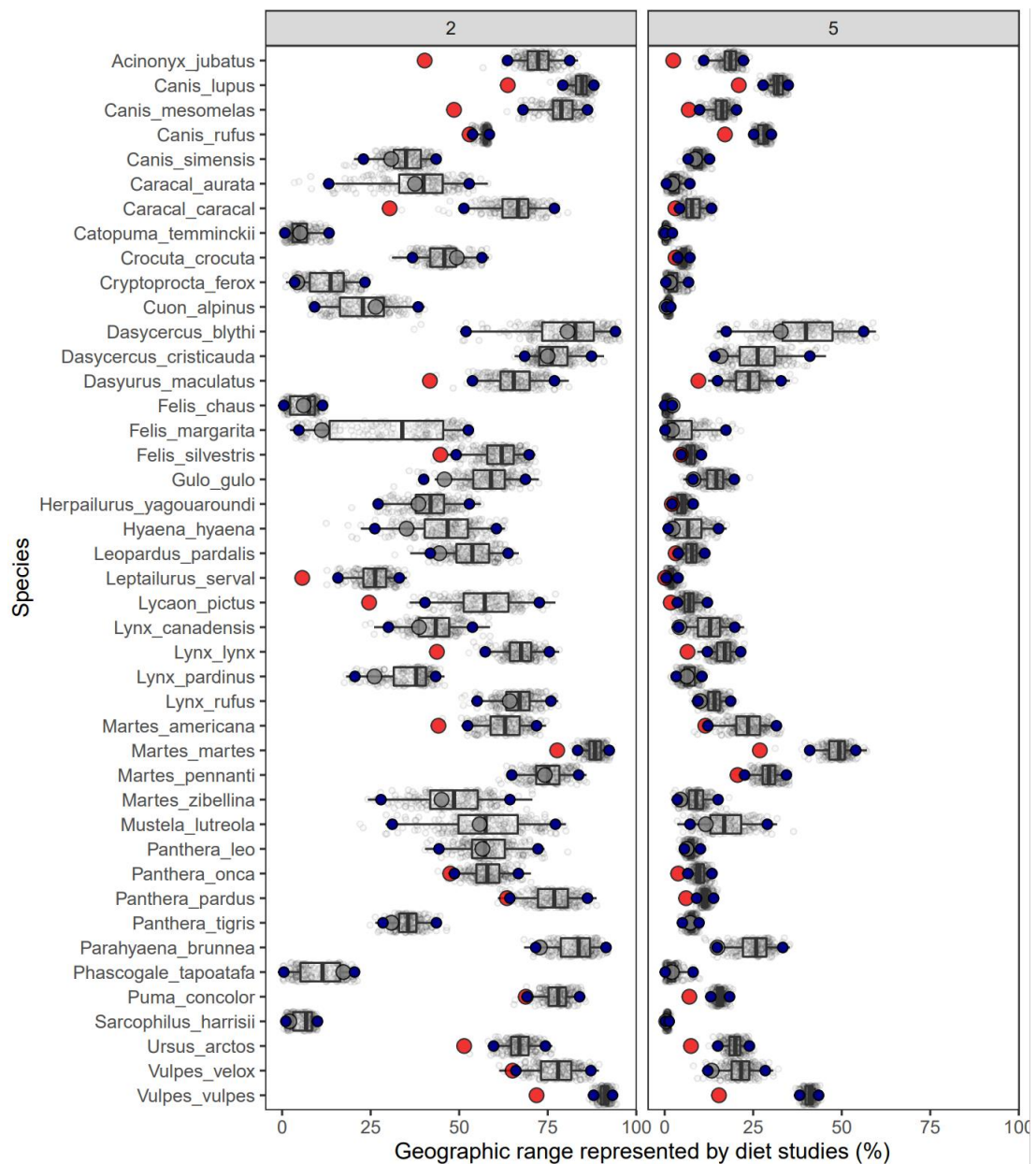


Figure A5.7 | Species-level geographic range representation of actual studies compared to 200 simulations of randomly distributed studies across their geographic range. Each simulation (transparent grey points and boxplots) is shown with the 95% upper and lower confidence intervals (blue points). Species with significantly lower range representation from actual studies compared to random are shown in red, with non-significant range representations shown with large grey points when environmental context is described with either two or five variables.

9.4.2 | Tables

TABLE A5.1 | Overview of abiotic and biotic variables that contribute to an area's environmental context and mediate the interactions a species forms within a community. A description of each variable used is provided, as well as the source of the raster layer for each variable. Each variable was selected as it has previously been shown to influence ecological community structures, resource availability, or both. We did not aim to provide a comprehensive review of the impacts of each variables, and therefore provide only key papers to support the variable selection decision.

Variable name	Variable description	Source	Influence on diet
Abiotic <i>Elevation</i>	Digital elevation model derived from global 250 m GMTED2010 and near-global 90 m SRTM4.1dev to estimate elevation (height above sea level).	EarthEnv	The elevational gradient of biodiversity is a key principle in biogeography, summarized concisely in (Lomolino, 2001) and (Gaston, 2000). Consumption of key prey taxa can vary with altitude (Zhou <i>et al.</i> , 2011; Díaz-Ruiz <i>et al.</i> , 2013).
<i>Annual mean temperature</i>	Trend in the annual average (mean) temperature in a raster cell.	WorldClim	Temperature correlates with latitude. Latitudinal patterns in the variation of dietary generalists (e.g. bears) are a well-studied ecological phenomenon (Vulla <i>et al.</i> , 2009; Bojarska & Selva, 2012).
<i>Temperature seasonality</i>	Trend in the seasonal variation (range) in the temperature in a raster cell.	WorldClim	Seasonal fluctuations in temperature and snow cover accumulation influences the amount of carrion carnivorous mammal diets (Needham <i>et al.</i> , 2014; Pereira <i>et al.</i> , 2014).
<i>Annual mean rainfall</i>	Trend in the annual average (mean) rainfall in a raster cell.	WorldClim	Rainfall influences water availability, the overall ecological community of ecosystems and biomes, and is a key biogeographical variable driving ecological community assembly (Gaston, 2000). Rainfall correlates with consumptions of certain food categories in tiger quolls (Andersen <i>et al.</i> , 2017).
<i>Rainfall seasonality</i>	Trend in the seasonal variation (range) in the rainfall in a raster cell.	WorldClim	Seasonal variation in species diets is common and widely studied. Increasing levels of aridity influences prey breadth and diet of leopards (Mann <i>et al.</i> , 2019). The level of rainfall in different seasons can influence the diets of bobcats and coyotes

				(McKinney & Smith, 2008). Female lions show differences in secondary prey selection in response to seasons with varying levels of rainfall (Davidson <i>et al.</i> , 2013). Dry seasons cause an increase in shrew and rodent consumption by small African carnivores (Ray, 1998). Rainfall seasonality is a large influence on Holarctic marten diets (Zhou <i>et al.</i> , 2011).
Biotic	<i>Small carnivore (<21kg) species richness</i>	Species richness of small carnivores in an area, as estimated from extent of occurrence maps. An estimate of the level of competition faced for resources within the small carnivore feeding guild.	IUCN	Competitive release from Tasmanian devils, following their population declines, is provided more large mammal prey and carcasses for quolls (Andersen <i>et al.</i> , 2017). However, multiple small carnivores co-occurring can in fact have a potential mutualistic relationship, hunting together to get otherwise unattainable prey species (Minta, Minta & Lott, 1992).
	<i>Large carnivore (>21kg) species richness</i>	Species richness of large carnivores in an area, as estimated from extent of occurrence maps. An estimate of the level of competition faced for resources within the large carnivore feeding guild. Also, an estimated of food subsidies provided to scavengers in the form of carcasses from large carnivore kills.	IUCN	The presence of large carnivores can influence the level of competition with similar sizes carnivores, limit prey resources for smaller carnivores, but also provide additional resources through carrion. In areas without jaguars, ocelots increased their consumption of larger prey which is attributed to the lack of competition with jaguars (Moreno, Kays & Samudio Jr, 2006).
	<i>Mammal species richness</i>	Species richness of all mammals, includes small and large carnivores, in an area, as estimated from extent of occurrence maps.	IUCN	Higher mammal species richness increases the diversity of prey species available for carnivores to consume. For large carnivore, increasing prey species richness increases their dietary breadth (i.e. levels of generalism) (Ferretti <i>et al.</i> , 2020).

<i>Human footprint index</i>	The Global Human Footprint Dataset of the Last of the Wild Project, Version 2, 2005 (LWP-2) is the Human Influence Index (HII) normalized by biome and realm between 1995-2005.	Last of the World, v2	Anthropogenic activity have far-effects on the ecosystem, including modifications to community assemblages and the resources available for species to consume (comprehensive review in (Sévêque <i>et al.</i> , 2020)). The consumptive and non-consumptive effects of apex predators are likely largely influence by the activity of humans in an areas (see comprehensive review in (Haswell <i>et al.</i> , 2017)).
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9.5 | Chapter 6

9.5.1 | Supplementary methods

Justification of functional traits selected for predators

Functional trait: Average predator body mass

Data type: *Numerical, Continuous*

Units: $\log_{10}(g)$

Body mass correlates with many species traits, including at the individual-level (e.g. metabolic rate (Brown *et al.*, 2004)) or at the population-level (e.g. abundance (White *et al.*, 2007)). Therefore, much ecological variation is captured in models that include body mass (Brown *et al.*, 2004). Across ecosystems, predator body mass is typically one to three times the magnitude of their prey (Woodward *et al.*, 2005), although predator-prey mass ratios vary between terrestrial and marine ecosystems (Brose *et al.*, 2006a; Tucker & Rogers, 2014), and also across taxa (Cohen *et al.*, 1993; Brose *et al.*, 2006a; Naisbit *et al.*, 2011). Predator-prey mass ratios not only influence interaction identity, but also strength (Emmerson & Raffaelli, 2004; Vucic-Pestic *et al.*, 2010). The strength of the relationship between predator and prey body-size ratios allows predictive modelling of interactions, including variation in the strength of interactions with prey of different body masses consumed by large predators (Gravel *et al.*, 2013).

Ecological interactions drive ecological processes (e.g. predation) and in turn ecosystem processes (e.g. nutrient dispersal) and are largely influenced by a species' body mass. Therefore, the distribution of body-sizes in communities influences whole food web structures and the functioning of ecosystems (Woodward *et al.*, 2005). The identity, strength, and distribution of ecological interactions among species influences the stability of food-webs, with the emerging interaction network from pair-wise species interactions being representative of entire ecosystem structure and function (Loeuille & Loreau, 2005; Brose, Williams & Martinez, 2006b; Berlow *et al.*, 2009).

Functional trait: Maximum prey body mass

Data type: *Numerical, Continuous*

Units: $\log_{10}(g)$

Resource consumption is largely influenced by body mass. Predators can influence prey population dynamic (Kuijper *et al.*, 2013) and prey abundance (Newsome & Ripple, 2015), and the identity of prey that predators hunt is largely determined by body mass (Carbone *et al.*, 1999). As large-bodied mammals can have cascading effects in ecosystems, a crucial aspect of a predator's ecological role within an ecosystem is determined by the largest prey species it can influence either directly or indirectly. For example, predators influence the distribution of nutrient pools in an ecosystem by stimulating the movement of prey (Schmitz *et al.*, 2010). Therefore, predators that can influence larger prey species, which have large home ranges and nutrient dispersal capacities, would have a wider impact on ecosystem nutrient dynamics (Berti & Svenning, 2020). Any species outside of predation are likely to have disproportionate impacts on an ecosystem (Sandom *et al.*, 2020), and therefore maximum prey size of predators is a crucial consideration for ecosystem functioning.

Predator-prey body mass relationships for mammals are well-established and commonly used (Carbone *et al.*, 1999). However, such relationships did not incorporate deviation between social and solitary predators (Fanshawe & Fitzgibbon, 1993; Lührs, Dammhahn & Kappeler, 2013). For example, the maximum prey size of a solitary and social predator of the same body mass would vary which is used for reconstructing extinct predator's prey range sizes (Van Valkenburgh *et al.*, 2016). This is also seen within species, whereby cooperative hunting with conspecifics increases prey size range and hunting success (Fanshawe & Fitzgibbon, 1993; Lührs *et al.*, 2013). As such, maximum prey body mass is unlikely to be captured by body mass alone when social and solitary predators of evolutionarily distinct taxa are present in a community and is the reason for separating this functional trait.

Functional trait: Locomotion

Data type: *Categorical, Nominal*

Categories used: *Cursorial, Scansorial, Generalized*

Animal locomotion is defined in animal behavioral studies (ethology) as: “*any of a variety of movements among animals that results in progression from one place to another*”. Locomotion is a broad term that can describe the morphological

mechanisms in which animals propel themselves in response to the effects of gravity. This can involve four physical environments: aerial, aquatic, fossorial, and terrestrial, the latter of which is the focus of this study. General locomotor adaptations for terrestrial mammal locomotion are “*not intended to be used as precise terms, but have a useful descriptive function*” (Brown & Yalden, 1973). Below, in bold are descriptive forms of locomotion that were considered for predators in this study.

1. **Cursoriality** is a commonly used description of locomotion, inferring adaptations to speed using a leg-swinging form of propulsion.
2. **Arboreal** species have morphological adaptations for tree-living have also occurred in some taxa (e.g. Primates), although not for all arboreal mammals (e.g. Tupaiidae).
3. **Scansorial** species show particular adaptations for climbing, rather than tree-living, and (e.g. sloths) (Brown & Yalden, 1973). Retractable claws observed in Felidae, and some other Carnivora (i.e. wolverines) are also adaptations of scansorial habits, as well as for hunting (Gonyea & Ashworth, 1975).
4. **Ambulatory** species do not show morphological adaptations for fast-movement on the ground (Álvarez, Ercoli & Prevosti, 2013). Such species are typically ambuligrade (i.e. flat-footed) in their stance, use economical gaits (movements or leg propulsions) which are symmetrical (i.e. bears).
5. ‘**Generalized**’ locomotion describes species with morphologically intermediate traits between two categories. For example, previous assessment for an extinct mustelid found it intermediate between a bounder (i.e. weasel) and scansorial (i.e. marten) (Schutz & Guralnick, 2007), with the extinct mustelid described as having a ‘generalized’ locomotion.

The speed at which an individual can move through a landscape to search for, and acquire, resources is by its locomotion. **Cursorial** species can travel fast across the landscape, searching for resources over a larger area, in comparison to **ambulatory** species which are typically slow-moving. **Scansorial** species can access resources in trees which would be otherwise only be available to species without climbing adaptations when arboreal resources come to the ground.

Functional trait: Bite force

Data type: *Numerical, Continuous*

Units: *Bite Force Quotient (BFQ; force of bite at canines, relative to body mass)*

The diet and feeding behavior of carnivorous animals can be inferred by bite force (Huber *et al.*, 2005). In predators, prey-size is limited by external forces that skull and mandible must endure from struggling prey (Thomason, 1991). Furthermore, they must then dismember the kill for consumption. Among living mammalian carnivores, bite force quotient (force at canines, relative to body mass; BFQ) has been used as a broad indicator of relative prey size and feeding ecology. Although, it may not necessarily be useful for predicting this for species with atypical morphologies (e.g. aardwolf) (Wroe, McHenry & Thomason, 2005). Phylogenetic differences in skull morphology occur between marsupial and placental predators and is therefore an important consideration as a predator functional trait due to the indication of the ecology of predators (Wroe *et al.*, 2005).

Functional trait: Hunting method

Data type: *Categorical, nominal*

Categories: *Pursuit, Pounce-pursuit, Ambush*

Foraging methods can influence the type and amount of resources available within an ecosystem (Huey & Pianka, 1981). Mammalian predators employ hunting methods influenced by morphological traits, which likely arise through co-evolutionary arms-races with prey. Active predators move continuously, looking for prey, sit-and-pursue predators stay hidden and attack approaching prey, whilst sit-and-wait predators stay hidden and wait for prey to encounter them; the latter are also described as ‘ambush’ predators (Huey & Pianka, 1981; Preisser, Orrock & Schmitz, 2007). For active predators, there are morphological trade-offs between maximizing running speed and efficiency and those that maximize grappling ability and fighting performance (Kemp *et al.*, 2005). Forelimb adaptations that promote effective prey handling (wide elbow joints to grapple prey) conflict with those for sustained pursuit (narrow elbow joints adapted for stabilizing high-speed motion) (Andersson 2004).

Prey species likely need to be adapted to these different hunting methods, which can be seen in African savannah herbivores whereby evolution of high-speed locomotion is influenced by the vulnerability to high-speed pursuit predators (Bro-Jørgensen, 2013). This response is just one part of a multi-response sequence of a prey responding

to a predator: predator detection (level 1), appropriate response (level 2), and effective response that leads to avoidance (level 3) (Carthey & Banks, 2014). In novel ecosystems, prey species may not be adapted to novel predators during the ‘response’ level of the sequence (Carthey & Blumstein, 2018) as evolutionary responses may be adapted to different hunting methods to the novel predator(s) (Carthey & Banks, 2016). For these reasons, hunting method is a key trait for identifying the ecological functions of predators, in particular in novel ecosystems.

Functional trait: Hunting group size

Data type: *Categorical, Ordinal*

Category order: *Solitary (1), Flexible (2), Social (3)*

While predator-prey body mass relationships for mammals are reasonably well established (Carbone *et al.*, 1999), such relationships do not take into variation influenced by social versus solitary hunting behavior (Fanshawe & Fitzgibbon, 1993; Lührs *et al.*, 2013). For example, the maximum prey size of a solitary and social predator of the same body mass would vary which is used for reconstructing extinct predator’s prey range sizes (Van Valkenburgh *et al.*, 2016). This is also seen within species, whereby cooperative hunting with conspecifics increases prey size range and hunting success (Fanshawe & Fitzgibbon, 1993; Lührs *et al.*, 2013). Therefore, species which have evolved group-hunting tactics are likely able to influence larger-bodied species than a species of the equivalent size, with potentially greater overall impacts on ecosystem disturbance and processes (see maximum prey size for further information and references).

Functional trait: Fecundity (controlling for reproductive group size)

Data type: *Continuous, Numerical*

Units: $\frac{\text{average litter size} \times \text{average litters per year}}{\text{average reproductive group size}}$

Predator behaviour (functional responses) can also be influenced by prey population size (numerical response) (Holling, 1959). Beyond behavior, predator and prey population dynamics can be influence by fluctuations in abundance of one another (Wangersky, 1978). The influence of population sizes is an important consideration

for the intrinsic effect of species' population in an ecosystem, highlighted by high mesopredator abundances on prey populations (Crooks & Soulé, 1999; Baum & Worm, 2009).

Population dynamics are influenced by life-history traits, one of which is the number of offspring per year, often referred to as fecundity. Fecundity has been calculated previously as the product of average litter size and number of litters per year (Thompson, 1987). In apex predators, top-down pressures on populations occur through self-regulation, and therefore their own population influences overall population fecundity (Wallach *et al.*, 2015a). This varies between species, although for social species can be maintained by infanticide by dominant individuals. In Corbett (1988) (Corbett, 1988), an observation of a pack of dingoes showed infanticide of all female's offspring by an alpha female, except for her own. However, in hunted populations of social canids, group size can decrease (Valdmann, Laanetu & Korsten, 2004), which likely increases the number of reproducing pairs, overall population fecundity, and subsequent top-down effects on prey populations. To control for these effects on population fecundity of a social, apex predators, we add an additional parameter to the equation to control for group size, whereby the average fecundity is controlled for by average reproductive group size, assuming not all individuals of a population participate in reproduction

For our study, this was an important consideration as phylogenetic differences traits between marsupials and predators (e.g. metabolic rate (Mcnab, 2005)) may be reflected in life-history traits. Thompson (1987) noted for 42 marsupial and 42 placental species that small (<400g) and large (>10kg) marsupials have lower natural rates of increase, calculated using fecundity and considering age of reproduction, than placentals. It was also noted that life-history strategies are broadly similar for intermediate-sized (1-5kg) marsupial and placental predators. However, despite differences observed in certain life history traits (e.g. pregnancy length, size of offspring at birth) reproduction rates scale similarly with body mass for placental and marsupial species (Hamilton *et al.*, 2011). Despite these reflecting average trends across marsupial and placental mammals, variation in such relationships may reflect differences between predators in our study.

Justification for thylacine prey body mass ranges

The ecological role of thylacines is widely debated, particularly in terms of what extant species is a suitable taxon substitute. Although, very recent research has shown that canids that are small-prey specialists (i.e. jackals and, to an extent, foxes) would make a reasonable proxy (Rovinsky *et al.*, 2020, 2021). However, we relied on descriptions from morphological analyses of thylacines, as well as anecdotal hunting behaviour, to estimate body mass thresholds for dietary importance categories. Analyses of skull and limb morphologies suggest they were similar to smaller canids (e.g. coyotes, jackals and foxes), and likely specialized on the small-medium size (1-5kg) prey species that are also associated with them in fossil deposits (Werdelin, 1986; Jones & Michael Stoddart, 1998). The reliance on small-medium prey was also concluded in Wroe *et al.* (2007), following computer simulations of cranial stress handling, but added that maximum prey mass for thylacines was comparable to solitary dingoes but lacked the capacity that dingoes have to handle stress from larger prey. Anecdotal prey lists for thylacines would suggest that they hunted prey between 1-30kg and were potentially trophically similar to Tasmanian devils (Paddle, 2000; Jones, 2003), and potential overlap of prey with Tasmanian devils and tiger quolls has also previously been shown (Attard *et al.*, 2011), despite thylacines having a larger body mass. Wroe *et al.* (Wroe *et al.*, 2007) note that, at 30kg, thylacines are larger than the 21.5kg threshold for reliance on large prey shown in terrestrial *Carnivora* (Carbone *et al.*, 1999) even after correcting for lower metabolic rate of marsupials. Yet, this argument does not consider variation in thylacine body mass ranges from 15-30kg (Jones, 2003), and at the lower end of this estimate on the mainland (Letnic *et al.*, 2012a). Regardless, the reliance of relatively small prey, given its body mass, is thought to have made thylacines particularly susceptible to disturbance (Wroe *et al.*, 2007). We conservatively estimated thylacine common prey (DI = 3) ranged from 1-5kg, occasional prey (DI = 2) from 1-30kg, and with rare prey (DI = 1) extending to a minimum that equals dingoes and maximum prey size of solitary dingoes (46kg, i.e. red kangaroos).

Justification of metrics used to describe food web structures

Network metrics were calculated using the ‘*omnivor*’ and ‘*NetIndices*’ packages (Soetaert *et al.*, 2015; Violet & Gravel, 2019) and are commonly used to describe network structures. We touch upon our justifications for using these metrics, although a comprehensive overview of some of these metrics are available in Tylianakis *et al* (2010). Tylianakis *et al* (2010) state that “....*conservation of complex emergent properties such as network stability will likely require monitoring of a suite of metrics*”, which influenced our decision to incorporate multiple network metrics in descriptions of network structural change.

Number of interacting nodes

Nodes represent species in an interaction network, with edges (links between nodes) reflecting a direct interaction between the two species. The number of species reflects the size of the network (Tylianakis *et al.*, 2010).

Mean body mass of species in network

As explained above, many ecological traits correlate with body mass. Incorporating the average size of species in ecological networks provides an ecological context to networks, takes into consideration the increasing impacts of large-bodied species in ecosystems and whether predators exist that can hunt them.

Number of links

The total number of links in a network may be referred to as the ‘interaction diversity’ or ‘interaction richness’ (Tylianakis *et al.*, 2010). This is comparable to measures of species richness in that biodiversity of a community is more influenced by composition (abundance and evenness) and, in the case of networks, the distribution of links in a network, or level of connectance.

In Tylianakis *et al* (2010), the number of links is suggested to represent the rate of ecosystem processes, and stability through time. In bipartite networks, more links in antagonistic networks (e.g. predator-prey) can represent increased herbivore suppression. However, this does not take into consideration the effects of interference competition of consumers on resource acquisition. Number of links may also reflect resilience in an ecosystem, whereby the loss of one species and its interactions are more likely to be compensated by the presence of another species with potentially

similar interactions (the insurance hypothesis; Yachi and Loreau (1999)). This metric is sensitive to species richness (Goldwasser and Roughgarden, 1997; Bersier et al., 1999; Nielsen and Bascompte, 2007).

Link density

Link density describes the average number of links belonging to a given species in the network (Tylianakis *et al.*, 2010). Broadly, the number of links per species describes the degree of generalism of species present in a network and is useful for comparing network structures of different sizes. This metric is sensitive to species richness and sampling intensity (Bersier, Dixon & Sugihara, 1999).

Connectance

Network connectance is measured as a proportion of the number of links in a network, relative to the number of potential links between all nodes in a network (Tylianakis *et al.*, 2010). This also broadly represents the overall degree of generalism of species within a network, whereby increasing connectance means an increased level of generalism among species. Lower connectance reflects specialist pairings between individual, or more likely groups of, species. The level of generalism influences the level of resilience whereby the loss of one species is likely buffered by the presence of another species (Tylianakis *et al.*, 2010).

Compartmentalisation

Compartmentalisation, often referred to as ‘modularity’, reflects subgroups of closely interacting species within larger interaction networks, with few weak interactions occurring between subgroups (May, 1973). Compartmentalization is thought to be a result of coevolution (i.e. trophic specialization; (Prado & Lewinsohn, 2004)), and is thought to be more common in antagonistic networks.

Intermediate species

The percentage of species that have both a resource and consumer in a food web (Baiser *et al.*, 2012; Violet & Gravel, 2019). In the context of our paper, this would be a small-prey specialist, or ‘mesopredator’.

Nestedness

Nestedness indicates that the interactions of a particular species are a subset of interactions of another species. Therefore, the loss of subsets of interactions are unlikely to alter the overall structure of the food web.

Justification of metrics used to describe species' roles in food webs

Species in communities play different roles and are not necessarily equal in their contribution to processes and properties (Delmas *et al.*, 2019). The interactions a species forms with others in a community are argued to be the fundamental units driving ecological processes which are influenced by the species' trophic level, abundance, body size, or other ecologically meaningful organizing principles (Delmas *et al.*, 2019). In interaction networks, it is possible to look at the properties of species (nodes) and their role within that network by assessing level of centrality – their position in a network. We used the average size of interacting species for a predator to indicate trophic level, as well as four measures of centrality recommended in Delmas *et al.* (Delmas *et al.*, 2019): degree centrality, closeness centrality, betweenness centrality and eigenvector centrality. These measures of centrality are commonly used to assess the trophic positioning and influence on a network. For example, such node-level measures have been used to assess the role of species in marine food webs (Navia, Cortés & Mejía-Falla, 2010; Bornatowski *et al.*, 2014), salt marshes (Anderson & Sukhdeo, 2011; Jiang & Zhang, 2015), paleoecological food webs (Lozano, Mateos & Rodríguez, 2016)

Average size of prey species (g)

The average body mass of the species in which it interacts with in a network. This is to give an idea of trophic positioning within the network, and because the ecological effects of a predator are more pronounced at the ecosystem level when interacting with larger prey.

Degree centrality

Degree centrality ($C_D(i) = k_i$; Freeman, 1977) is a measure of the number of edges (interactions) a node (species) has with other nodes. To ensure comparability between species' centrality measures, the absolute value must be normalized to a relative value (Freeman, 1979), which is expressed as

$$relative\ C_D = C_D/k_{max},$$

where k_{max} indicates the maximum number of edges a node can ($N-1$).

Closeness centrality

Closeness centrality (C_C) measures how close a node is to all other nodes, taking into consideration the entire network structure (Freeman, 1978). This shows the shortest path length between node pairs and indicates how quickly a node could influence the whole network, therefore nodes with higher C_C are close to all other nodes and will influence other nodes. The node with the highest C_C is closer to all other nodes than any other nodes and will thus affect more rapidly the overall network if, for example, there is a perturbation (Estrada & Bodin, 2008). Formally, C_C is defined as

$$C_C = \sum_{j \neq i} \frac{n-1}{d_{ij}},$$

where d_{ij} is the shortest path length between nodes i and j , and n is the number of nodes.

Betweenness centrality

Betweenness Centrality (C_B) (Freeman, 1978) describes the number of times a species is between a pair of other species, i.e. how many paths (either directed or not) go through it.. Nodes with high C_B values are considered as module connectors in modular networks. The value of C_B is usually normalized by the number of pairs of species in the network excluding the species under focus, and is measured as

$$C_B(i) = 2 \times \sum_{j < k; i \neq j} \frac{g_{jk}(i)/g_{j,k}}{(n-1)(n-2)}$$

where g_{jk} is the number of paths between j and k , while $g_{jk}(i)$ is the number of these paths that include i .

Eigenvector centrality

Eigenvector centrality represents the overall effects of each species on all of its partners simultaneously (Bonacich, 1987). It has been used to represent the importance of species in interaction networks whereby their removal is likely to have the greatest impacts throughout a network (Allesina & Pascual, 2009). The scores of each species represent the first eigenvector of the adjacency matrix that describes pairwise interactions. Species with high eigenvector centrality values therefore exist in densely populated substructures in the food web (Anderson & Sukhdeo, 2011).

9.3.2 | Figures

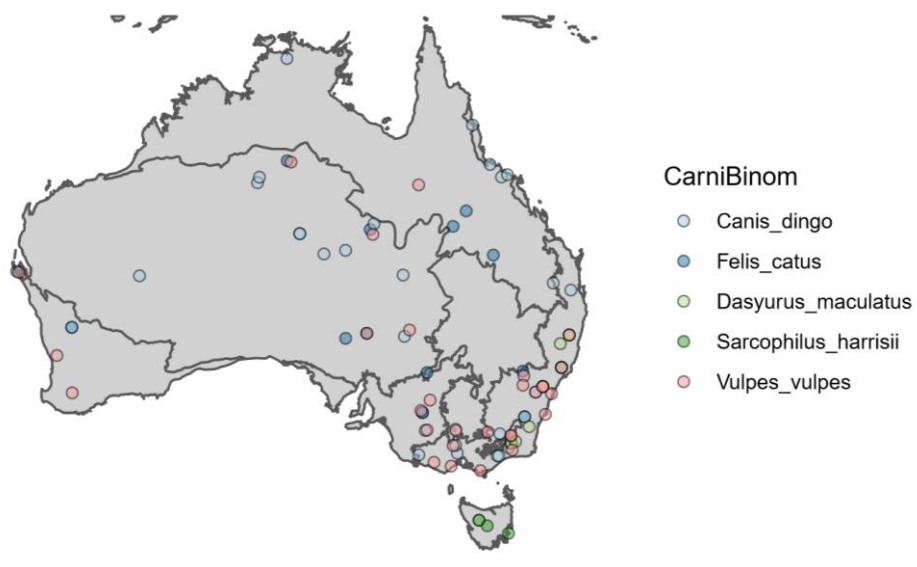


FIGURE A6.1 | Location of the study sites where field data was originally collected on the diets of extant Australian predators.

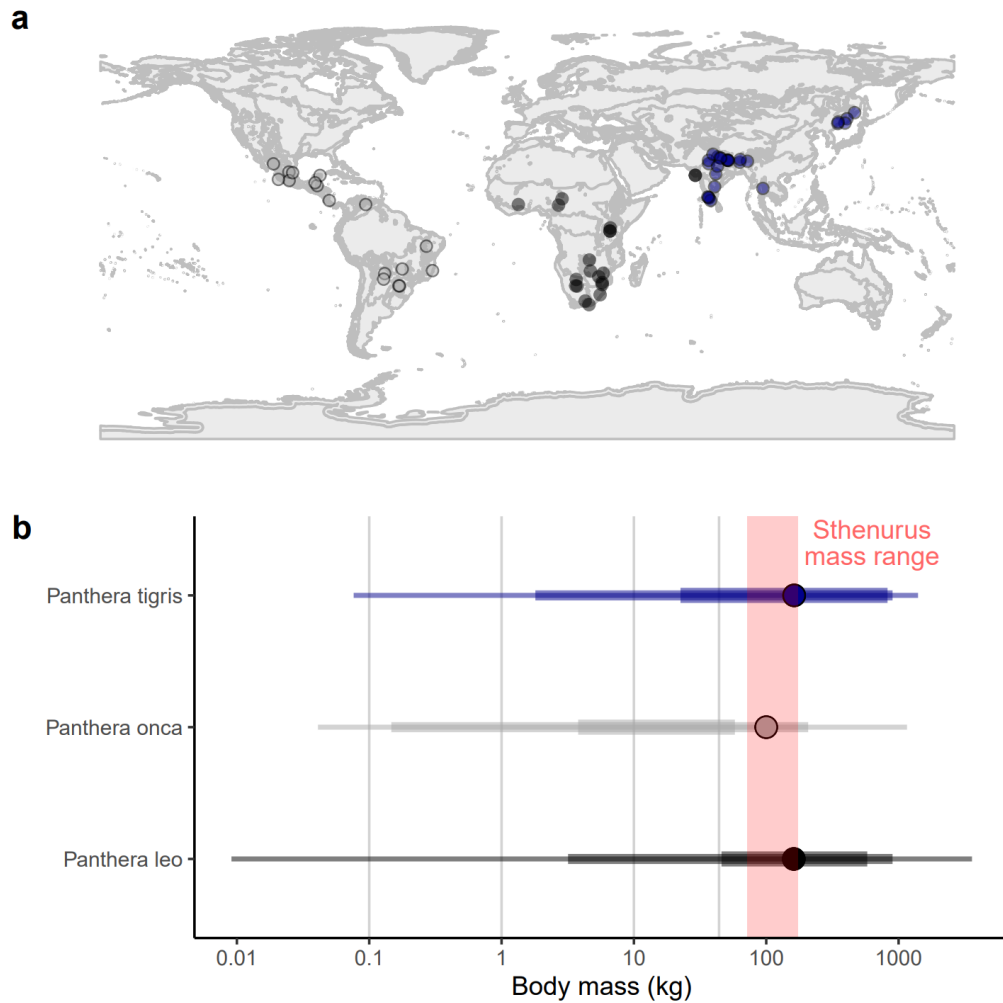


FIGURE A6.2 | Diet information on large felids as potential proxies for the diet of marsupial lions. (a) Location of the study sites where diets of tigers (blue), lions (black), and jaguars (grey) were originally studied, and data extracted from CarniDIET 1.0 (Middleton *et al.*, 2021). (b) Body mass of predators (circles) and the body mass thresholds of potential prey that could be consumed commonly (20% of diet; thickest line), occasionally (<20% and $\geq 5\%$ medium thickness line), and rarely (<5%; thinnest line). Vertical lines indicate the prey body mass category breaks used in the main Australian study. The red rectangle indicates the body mass range of taxa within the genus *Sthenurus* and are considered to have been common prey of marsupial lions.

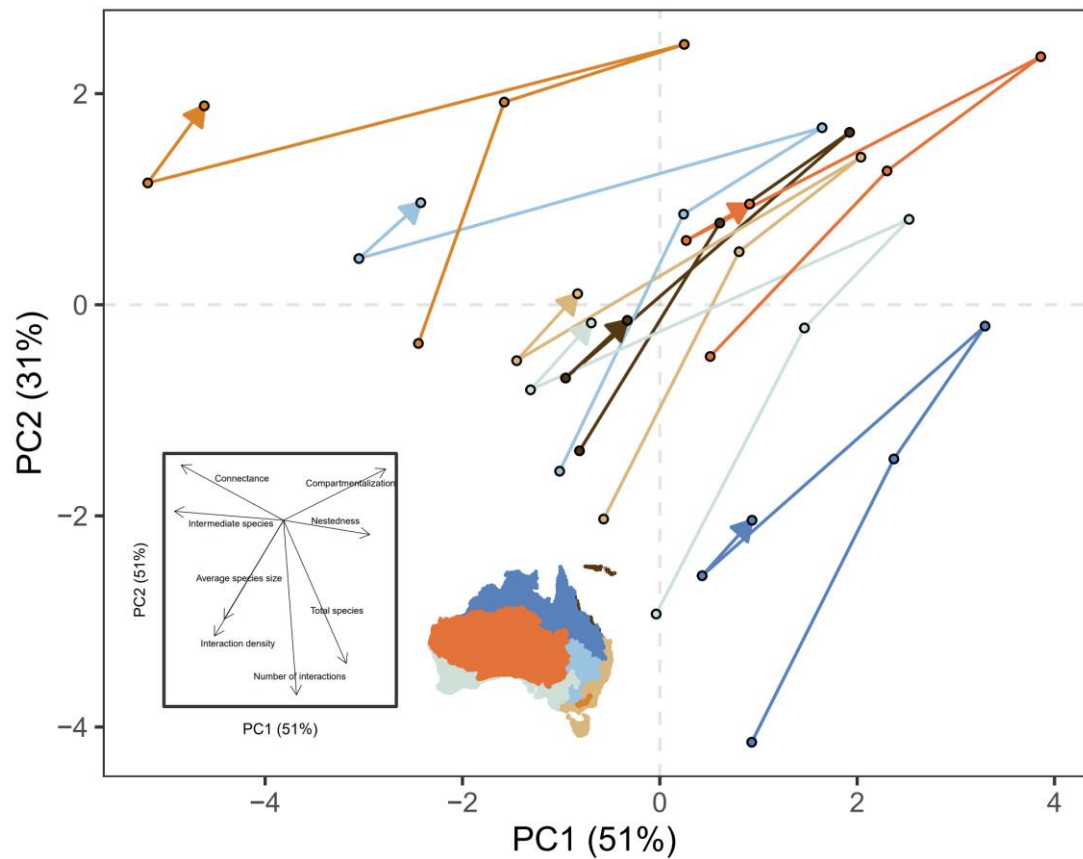


FIGURE A6.3 | Principal component analysis showing changes in metrics describing the structure of Australian food web across four time periods for each of seven biomes (colors of lines and points indicate biomes on the inset map of Australia) and following dingo persecution if unprotected (final line with arrow). The inset plot shows the PCA loadings with eight input network structure metrics. Changes in each biome's network metrics are shown in Fig. S5.

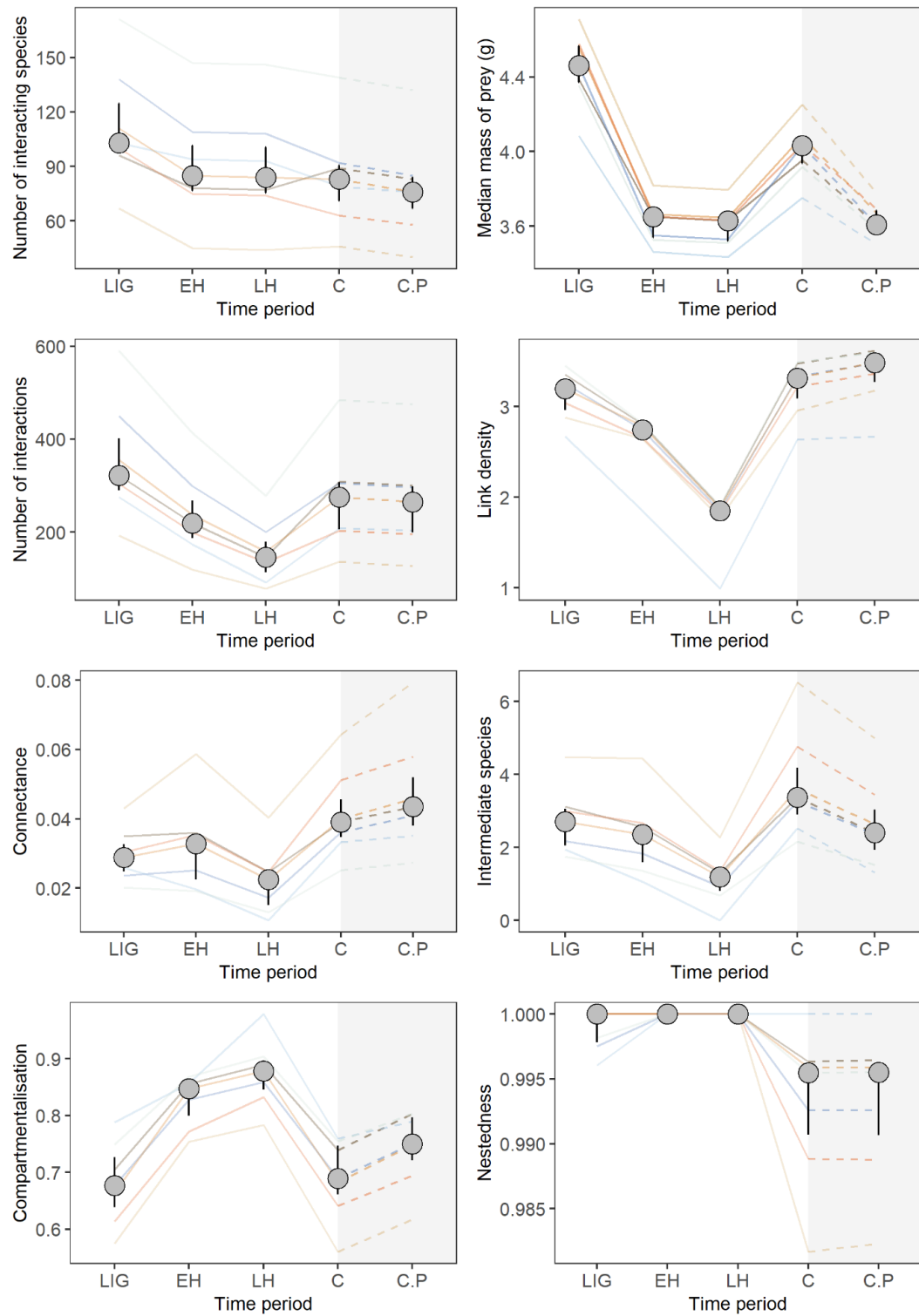


FIGURE A6.4 | Change in network-level metrics between each time period and the transition from dingoes being protected (C) to persecuted (C.P) in current-day food webs.

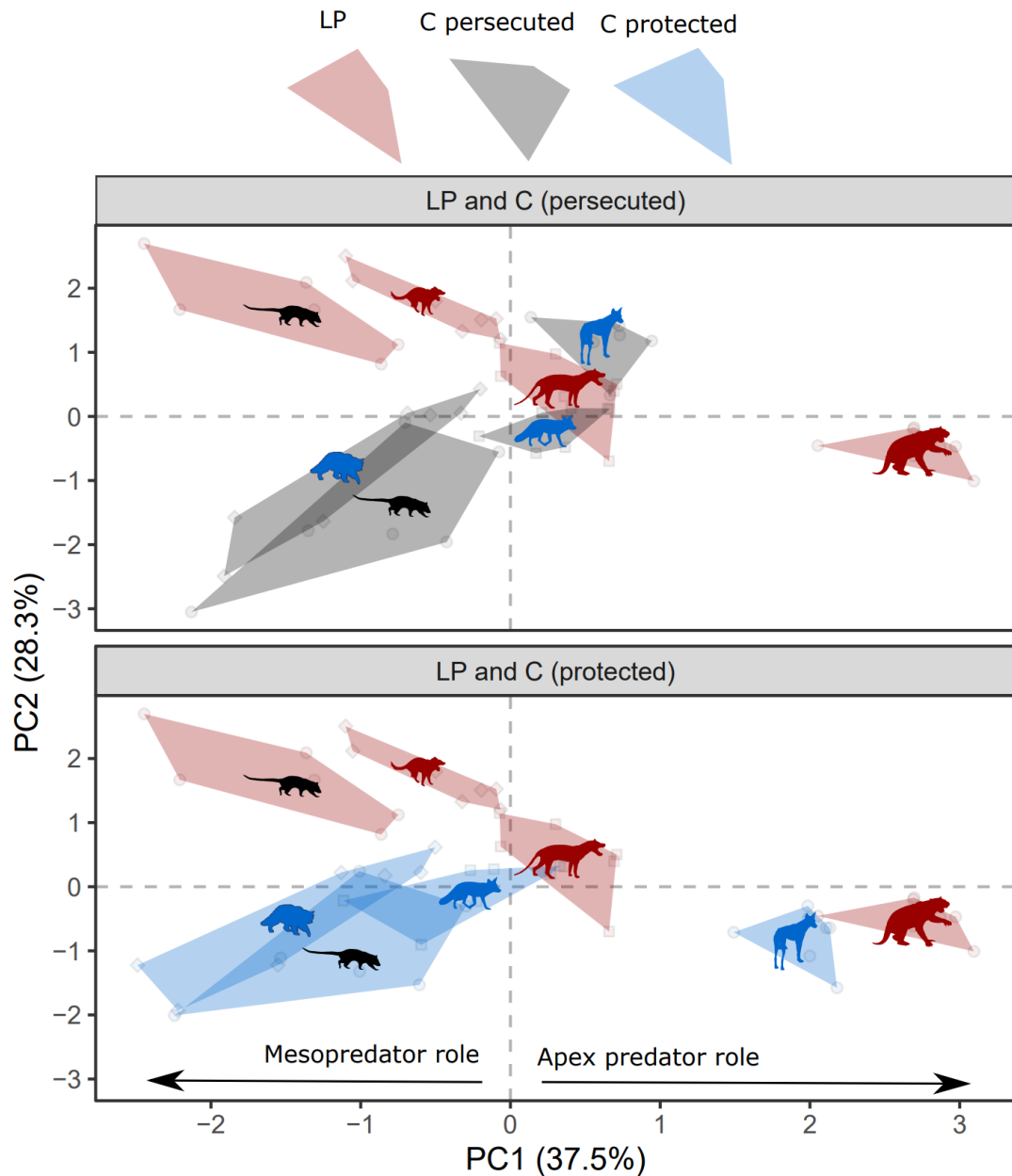


FIGURE A6.5 | Predator ecological roles in Late Pleistocene (LP) and current-day (C) food webs, shown separately for C food webs with persecuted and protected dingo populations. Polygons reflect the convex hull of the biome-level variation for each predator's ecological roles (highly transparent circles) for different time periods or current-day scenarios. Colours of predator icons indicate their status of extinct (red), extant-native (black), or recently established (blue). Predator icon locations indicate the center of the convex hull.

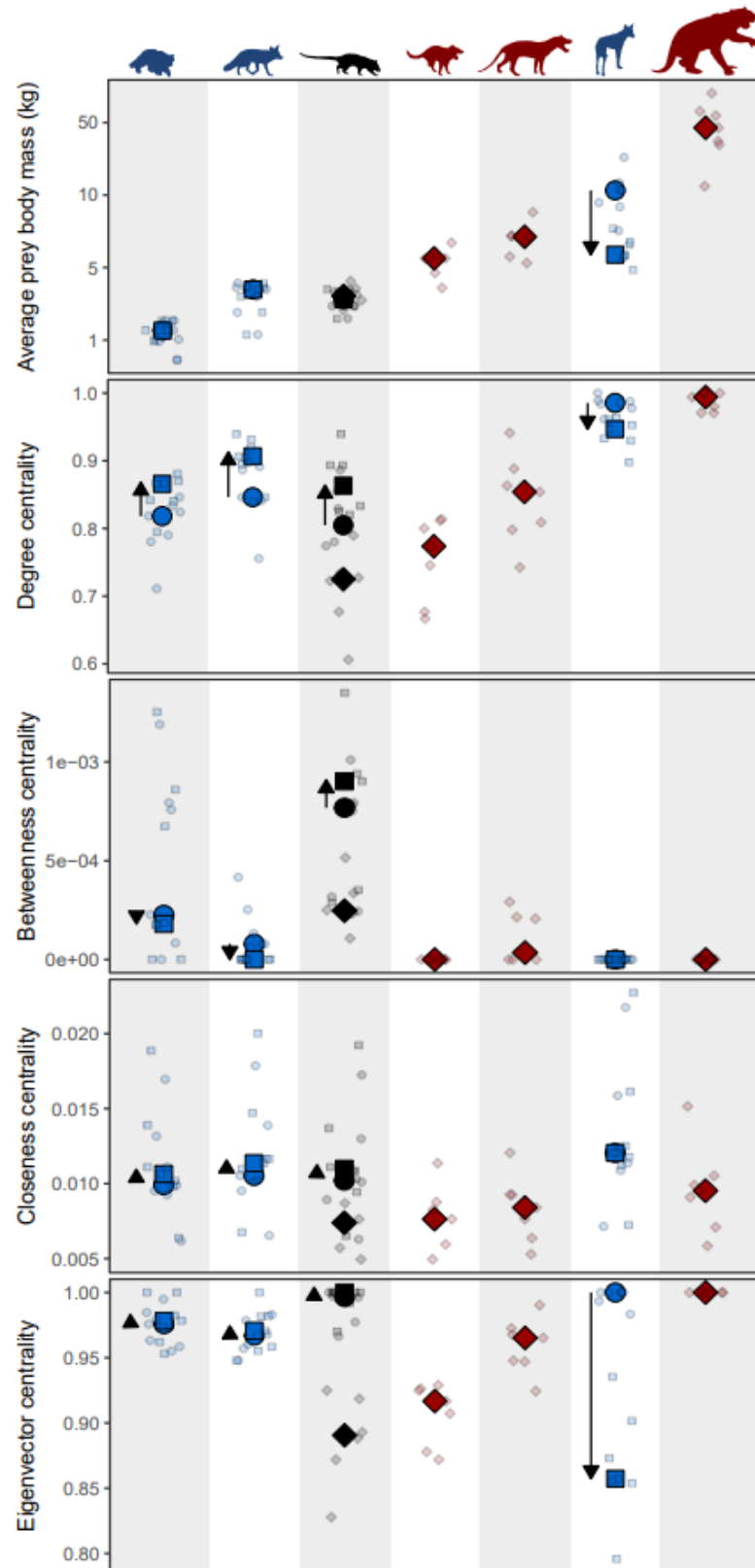


FIGURE A6.6 | Species-level metrics describing an aspect of each predator species' ecological role (blue = introduced placental, red = extinct marsupial, black = extant marsupial) in the LP food web (diamond) or current-day food webs (circle/square). Arrows indicate transitions in species-level metrics in current-day food webs when dingoes go from being protected (circle) to being persecuted (square).

9.3.3 | Tables

TABLE A6.1 | Changes in the number and average strength of potential interactions between mammalian predator and prey species from mainland Australia's food web in the LP to the current-day across five prey body mass categories. Replacement values are also shown visually in Fig. S3. Three forms of replacement were considered: 'predator replacement, whereby a lost interaction between an extant native prey species and extinct predator is replaced by a recently established predator; 'prey replacement, whereby a lost interaction between an extinct prey species and extant native predator is replaced by a recently established prey species; 'predator & prey replacement, whereby a lost interaction between an extinct predator and extinct prey has been replaced by an interaction between a recently established predator and recently established prey species.

Status (Extinct/Extant/Native)		Changes to interactions across five body mass categories in mainland Australia's food web									
		<0.1kg		0.1-1kg		1-10kg		10-44kg		>44kg	
Predator	Prey	Number	Strength	Number	Strength	Number	Strength	Number	Strength	Number	Strength
<i>Predator replacement</i>											
Extinct	Native	243	1.3	117	1.3	162	2.2	46	2.3	2	2.0
Established	Native	262	2.2	111	2.7	156	2.6	23	2.9	1	3.0
	Changes:	+19	+0.9	-6	+1.4	-6	+0.4	-23	+0.6	-1	+1.0
<i>Prey replacement</i>											
Extant	Extinct	5	2.0	9	2.3	5	3.0	4	2.0	0	0.0
Extant	Established	1	2.0	2	2.5	4	2.5	0	0.0	0	0.0
	Changes:	-4	0	-7	+0.2	-1	-1	-4	-2	0	0
<i>Predator and prey replacement</i>											
Extinct	Extinct	15	1.3	30	1.3	15	2.1	26	2.0	21	3.0
Established	Established	3	2.3	6	2.7	12	2.7	1	3.0	7	2.0
	Changes:	-12	+1.0	-24	+1.3	-3	+0.5	-25	+1.0	-14	-1.0

TABLE A6.2 | Potential strength of intraguild interactions between mammalian predators in Australia. Top-down control from extinct predators (*) are reasonable assumptions, given that this is observed in ecosystems across the world. Intra-specific interactions are in black, and interactions between predators that do not occur in the same time periods are in red. Intra-guild interactions are also considered for unpersecuted (UP) and persecuted (P; grey) dingoes, separately.

	Marsupial lion	Thylacine	Dingo	Tasmanian devil	Tiger quoll	Red fox	Feral cat
Marsupial lion		3*		3*	3*		
Thylacine	0			3*	3*		
Dingo (UP)					3	3	3
Tasmanian devil	0	0			1		
Tiger quoll	0	0	0	0		0	1
Red fox			0		3		3
Feral cat			0		1	0	
Dingo (P)					0	0	0

Marsupial lion

Thylacine, Tasmanian devil, Tiger quoll: As a large, apex predator, it is assumed marsupial lions had top-down effects on these smaller predators.

Thylacine

Tasmanian devil, tiger quoll: Assumed to have top-down effects on smaller predators.

Dingo (protected; persecuted interactions are justified in the main text)

Red fox: In the absence of dingoes, red foxes are typically found in higher abundances (Newsome *et al.*, 2001; Letnic & Koch, 2010).

Feral cats: Dingoes could influence population sizes of cats (Kennedy *et al.*, 2012; Schroeder *et al.*, 2015), and can suppress both the abundance and activity of feral cats which benefits a native rodent (Gordon *et al.*, 2015), although these effects appear less persistent than with foxes and we note that these effects are likely context dependent (Fancourt *et al.*, 2019).

Tiger quolls: Interactions between dingoes and quoll species are poorly understood, although spotted-tailed quolls appear in dingo scats and competition likely occurs (Glen & Dickman, 2005).

Tasmanian devils

Tiger quolls: Not widely understood but mostly competitive interactions (Pemberton *et al.*, 2008).

Tiger quolls

Feral cats: Exploitative competition for food resources and den sites (Glen & Dickman, 2005)

Red fox

Feral cats: Red foxes can control some aspects of feral cat behaviour and various other studies under various ecological contexts have shown cat activity or abundance to increase following red fox removal (see review in Molsher *et al.* (2017)). Meta-analyses of red fox removal also shows cats increased following removal (Hunter *et al.*, 2018).

Tiger quolls: Competitive interactions occur but also changes in behaviour that is thought to force quolls to persist at lower population densities (Glen & Dickman, 2005)

Feral cat

Tiger quolls: Exploitative competition for food resources and den sites (Glen & Dickman, 2005).

TABLE A6.3 | Directions along the first two axes of the PCoA predator functional trait space along which functional trait values changed. Goodness of fit (squared correlation coefficient, r^2) between traits and axes are given alongside empirical p -values of the fit between traits values and PCoA axes. Traits are ordered from ‘strongest’ (top) to ‘weakest’ (bottom) in their structuring of functional space according to r^2 . Categorical traits are given with the factor levels in brackets. Significant traits ($p < 0.05$) are indicated by *.

Traits	A1	A2	r^2	p -value
Maximum prey size, $\log_{10}(g)$	-0.95	-0.32	0.96	<0.001*
Body mass, $\log_{10}(g)$	-0.94	-0.33	0.90	0.004*
Bite force quotient	-0.99	0.12	0.88	0.01*
Hunting method (Pursuit)	0.14	-0.99	0.83	0.052
Hunting group size	-0.42	-0.91	0.81	0.02*
Hunting method (Ambush)	-0.38	0.93	0.77	0.04*
Locomotion (Cursorial)	0.41	-0.91	0.71	0.03*
Locomotion (Generalized)	-0.71	0.71	0.69	0.04*
Fecundity	0.96	-0.26	0.60	0.07
Locomotion (Scansorial)	0.62	0.78	0.26	0.57
Hunting method (Pounce-pursuit)	0.99	0.07	0.16	0.67

TABLE A6.4 | Importance of the first two principal components (82% variance explained) used to describe the structure of mainland Australia’s food webs across four time periods.

	PC1	PC2
<i>Component importance</i>		
Standard deviation	2.00	1.55
Proportion of variance	0.51	0.31
<i>Network metric</i>		
Number of interactions	-0.08	-0.61
Number of species	-0.29	-0.49
Number of intermediate species	0.48	0.002
Connectance	0.46	-0.16
Compartmentalisation	-0.44	-0.22
Interaction density	0.29	0.43
Nestedness	-0.38	0.03
Average species size	0.17	0.35

TABLE A6.5 | Importance of the first two principal components (66% variance explained) used to describe the ecological roles of predators in mainland Australia’s food webs in the LP and current-day.

	PC1	PC2
<i>Component importance</i>		
Standard deviation	1.37	1.19
Proportion of variance	0.38	0.28
<i>Node metric</i>		
Eigenvector centrality	0.17	-0.69
Degree centrality	0.61	-0.29
Average prey size	0.61	0.04
Betweenness centrality	-0.47	-0.55
Closeness centrality	-0.07	0.35