THE ROLE OF THE MATRIX IN SHAPING EXTINCTION RISK AND CONSERVATION OPPORTUNITIES FOR TERRESTRIAL MAMMALS

by

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Abstract

The global biodiversity crisis, driven primarily by habitat loss and fragmentation, has traditionally led conservation efforts to focus almost exclusively on primary habitats. However, the ecological importance of the matrix, defined as areas surrounding primary habitat, has remained largely overlooked.

In this dissertation, I used global-scale spatial analyses coupled with statistical modeling to (i) quantify how matrix condition influences the effects of habitat fragmentation on extinction risk for terrestrial mammals, (ii) compare the predictive performance of alternative habitat intactness models (patch-matrix, continuum, and hybrid models) for assessing extinction risk in terrestrial mammals, and (iii) map global patterns of terrestrial mammal species richness within the matrix to identify conservation opportunities beyond primary habitats.

My findings demonstrate that matrix condition plays a key mediating role in the relationship between habitat fragmentation and extinction risk, with greater predictive power than habitat loss or habitat amount alone. Moreover, I found that the predictive importance of fragmentation increases as matrix condition deteriorates, suggesting that managing or restoring the matrix represents a strategic conservation action to mitigate the negative effects of fragmentation on biodiversity. Additionally, the hybrid habitat intactness model—which integrates discrete habitat patches with continuous gradients of habitat quality—consistently outperforms traditional patch-matrix and continuum models, regardless of species' habitat specialization. Notably, the magnitude of the relationship between habitat intactness and extinction risk was greater when using the hybrid model, highlighting that integrating discrete and continuous habitat representations can improve extinction risk analyses and provide valuable insights for conservation. My results further reveal that hotspots of species richness within the matrix occupy only about 1% of Earth's terrestrial surface, yet could support more than half of all terrestrial mammal species. Matrix areas identified as having high conservation potential—based on overlapping richness hotspots—are primarily concentrated in tropical strongholds such as the Amazon Basin, Colombian Tropical Andes, Brazilian Atlantic Forest, and Albertine Rift. Importantly, many of these matrix areas face intense human pressures and remain inadequately represented within existing protected areas and other area-based conservation measures, underscoring their value as strategic opportunities for biodiversity conservation.

Collectively, my results highlight an urgent need for a paradigm shift in conservation strategies that explicitly recognize, manage, and restore matrix areas as integral components of global biodiversity conservation. Integrating the matrix into conservation planning closely aligns with international biodiversity frameworks, particularly Target 2 of the Kunming-Montreal Global Biodiversity Framework, which calls for restoring at least 30% of degraded terrestrial ecosystems to enhance ecological integrity and connectivity. Such integration could substantially improve biodiversity outcomes, ecosystem resilience, and landscape connectivity, ultimately making critical contributions toward reversing global biodiversity declines.

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Chapter 1: Introduction

Biodiversity—the variety of life forms across genes, species, and ecosystems—underpins ecological functions and services upon which human societies depend (Cardinale et al. 2012). These ecosystem services include nutrient cycling, climate regulation, pollination, and the provision of goods such as food, medicine, and freshwater (Cardinale et al. 2012, Díaz et al. 2019). Over the past century, however, biodiversity has declined globally at unprecedented rates, raising concerns about ecosystem stability and human well-being (IPBES 2019). Current extinction rates are estimated to be tens to hundreds of times greater than natural background levels, providing strong evidence that the Earth is undergoing its sixth mass extinction event (Barnosky et al. 2011, Pimm et al. 2014, De Vos et al. 2015, Ceballos et al. 2015).

Recent global assessments underscore the alarming magnitude of biodiversity loss. For example, vertebrate populations have declined by almost 73% since 1970 (WWF 2024), and 41% of amphibians, 27% of mammals, 21% of reptiles, and 12% of birds are currently classified as threatened on the International Union for Conservation of Nature (IUCN) Red List (IUCN 2025). These declines reflect profound ecological transformations driven primarily by human-induced pressures, including habitat destruction, overexploitation, climate change, pollution, and invasive species (Newbold et al. 2015, Maxwell et al. 2016, Jaureguiberry et al. 2022).

Terrestrial mammals

Among vertebrates, terrestrial mammals have been widely prioritized for monitoring broad biodiversity trends, given their ecological versatility, cultural significance, charisma, and functional roles within ecosystems (Ceballos and Ehrlich 2002, Cardillo et al. 2005, Hoffmann et al. 2011, Ripple et al. 2014). Terrestrial mammals contribute to ecosystem functioning by serving as top predators, keystone herbivores, seed dispersers, and ecosystem engineers (Estes et al. 2011, Dirzo et al. 2014). Their presence helps regulate vegetation structure, trophic dynamics, and ecological connectivity (Ripple et al. 2017, Galetti et al. 2018). For instance, the loss of large mammalian herbivores such as elephants (*Loxodonta africana*) in Africa and tapirs (*Tapirus terrestris*) in South America, as well as apex carnivores like wolves (*Canis lupus*) in the Northern Hemisphere and jaguars (*Panthera onca*) in the Neotropics, can lead to dramatic ecological changes through altered browsing, grazing, and predation dynamics (Estes et al. 2011, Ripple et al. 2017, Galetti et al. 2018). These losses can also disrupt trophic cascades by removing key predators that control prey populations, and reduce ecological connectivity by limiting seed dispersal and animal movement across landscapes (Terborgh et al. 2001, Dirzo et al. 2014).

However, despite their ecological importance, terrestrial mammals are experiencing widespread and accelerating declines. Recent global assessments estimate that up to 20% of terrestrial mammal species are at risk of rapid extinction (Cardillo et al. 2023), and numerous others not formally listed as threatened are already undergoing population declines and range contractions (Ceballos et al. 2017, 2020), reflecting broad vulnerability and reduced resilience to ongoing environmental disturbances.

In addition to these alarming trends, much of their remaining high-suitability habitat occurs outside the boundaries of protected areas (PAs)—geographical areas designated and managed primarily for biodiversity conservation (Dudley 2008)—further elevating their risk of extinction (Crooks et al. 2017, Cardillo et al. 2023). Anthropogenic pressures—such as agricultural expansion and hunting—have been identified as primary drivers of these trends, with the most severe impacts observed in the Indomalayan and Australasian biogeographic realms

(Hoffmann et al. 2011). Large-bodied species, characterized by slow reproductive rates, wide-ranging movements, and specialized habitat needs, have exhibited the most pronounced declines, underscoring their susceptibility to multiple forms of human pressure (Ripple et al. 2014, Dirzo et al. 2014, Benítez-López et al. 2017).

Habitat loss and fragmentation

Central to understanding the current biodiversity crisis is recognizing the extensive scale of human-induced habitat modification. Human activities have transformed between 75% and 95% of Earth's ice-free land surface, primarily through agricultural expansion, urbanization, resource extraction, and infrastructure development (Venter et al. 2016, Ellis et al. 2021, Ellis 2021). Habitat fragmentation—the breaking apart of continuous habitat into smaller and isolated patches—further exacerbates biodiversity loss by reducing habitat area, isolating populations, disrupting species interactions, and limiting organism movement and dispersal (Haddad et al. 2015). Consequently, fragmented landscapes can affect genetic diversity, population viability, species richness, and ecological resilience, making habitat fragmentation a central challenge for global biodiversity conservation (Haddad et al. 2015, Wilson et al. 2016, Pfeifer et al. 2017).

Terrestrial mammals are particularly vulnerable to habitat fragmentation due to their large spatial requirements, ecological specialization, and restricted dispersal abilities (Fahrig 2003, Crooks et al. 2017, Tucker et al. 2018). Fragmentation disrupts mammalian ecology by increasing habitat isolation, which restricts dispersal, limits access to habitat resources, and reduces gene flow, potentially leading to genetic bottlenecks and inbreeding depression (Cushman et al. 2006, Thatte et al. 2020). Empirical studies have shown that fragmentation intensifies edge effects—such as increased predation risk, altered species interactions, and microclimatic changes—that disproportionately affect mammalian populations and accelerate their declines (Pfeifer et al. 2017). Moreover, global analyses consistently indicate that terrestrial mammals experiencing higher levels of fragmentation within their geographic ranges face an elevated risk of extinction (Crooks et al. 2017, Ramírez-Delgado et al. 2022).

Historically, global conservation responses have predominantly focused on establishing PAs to mitigate biodiversity declines (Bruner et al. 2001, Rodrigues et al. 2004, Watson et al. 2014). Although the global PA network has significantly expanded over recent decades (Watson et al. 2014), it currently covers only around 16% of Earth's terrestrial ecosystems (UNEP-WCMC and IUCN 2025)—far short of the coverage necessary to effectively protect biodiversity (Allan et al. 2022). Furthermore, many PAs lack ecological connectivity and often fail to represent critical habitats adequately, particularly in regions experiencing intensive agricultural and urban development pressures (Allan et al. 2017, Geldmann et al. 2019). Thus, reliance solely on PAs is increasingly recognized as insufficient to halt biodiversity loss (Watson et al. 2014, Maxwell et al. 2020, Allan et al. 2022).

For terrestrial mammals, evidence suggests that existing PAs and targeted conservation actions—while critically important for many species (Pacifici et al. 2020)—remain insufficient to halt or reverse declining trends (Craigie et al. 2010, Di Marco et al. 2014a, Cardillo et al. 2023). For instance, previous research has shown that for every mammal species whose conservation status improved due to targeted interventions, approximately seven species deteriorated, primarily because conservation measures failed to adequately address major threats such as habitat loss, habitat fragmentation, habitat degradation, and hunting pressures (Hoffmann et al. 2011).

Recognizing these critical shortcomings, recent international policy initiatives, such as the Kunming-Montreal Global Biodiversity Framework (GBF), aim to conserve at least 30% of terrestrial and restore at least 30% of degraded ecosystems by 2030 (Obura 2023). Achieving these ambitious global conservation goals requires transformative strategies extending beyond traditional PA models (Watson et al. 2018b, Maxwell et al. 2020, Allan et al. 2022). Specifically, conservation efforts must incorporate biodiversity within human-modified landscapes, recognizing habitats previously considered marginal or unsuitable for conservation (Kremen and Merenlender 2018, Ellis 2019, Arroyo-Rodríguez et al. 2020, Britnell et al. 2023).

The matrix and landscape complexity

Habitat loss and fragmentation, long recognized as major drivers of biodiversity decline (Newbold et al. 2015, Maxwell et al. 2016, Jaureguiberry et al. 2022), have played a central role in shaping conservation theory and practice over recent decades (Ricketts 2001, Watson et al. 2005, Laurance 2008). Early conservation frameworks, informed by classic island biogeography theory, viewed fragmented terrestrial habitats as isolated 'islands' embedded within uniformly hostile 'matrix' environments (MacArthur and Wilson 1967, Haila 2002). Under this model, species richness and extinction risk were primarily determined by patch size and isolation, emphasizing straightforward colonization-extinction dynamics dependent on habitat area (MacArthur and Wilson 1967). As a result, traditional conservation strategies predominantly emphasized protecting large, intact habitat patches through networks of PAs (Margules and Pressey 2000, Martin et al. 2012), often regarding the surrounding matrix as either ecologically irrelevant or uniformly inhospitable.

However, a growing body of evidence has challenged this simplistic habitat-matrix dichotomy, revealing that biodiversity responses to habitat loss and fragmentation are more nuanced and context-dependent than previously recognized (Ricketts 2001, Laurance 2008, Prugh et al. 2008, Prevedello and Vieira 2010, Watling et al. 2011, Driscoll et al. 2013). These insights have inspired theoretical advances in landscape ecology, leading to frameworks such as countryside biogeography (Daily et al. 2001, 2003) and the landscape continuum model (Fischer and Lindenmayer 2006), which represent habitats within a gradient of ecological suitability rather than binary classifications of 'habitat' versus 'non-habitat.'

Empirical studies increasingly support this continuum perspective, demonstrating that the environmental characteristics of the matrix—defined as areas surrounding primary habitat patches—play a critical role in shaping species persistence, dispersal, and extinction risk (Prugh et al. 2008, Gardner et al. 2009, Prevedello and Vieira 2010, Watling et al. 2011, Driscoll et al. 2013, Boesing et al. 2018, Ferreira et al. 2018, Ramírez-Delgado et al. 2022). The matrix typically comprises landscapes modified or managed by human activities, such as agriculture, forestry, settlements, or infrastructure (Fahrig 2001, Franklin and Lindenmayer 2009). Beyond simply isolating habitat patches, the matrix provides supplementary resources, facilitates species movement and dispersal, and can buffer populations against disturbances depending on its composition and quality (Prevedello and Vieira 2010, Driscoll et al. 2013, Fletcher et al. 2024). For instance, human-modified habitats, such as secondary forests, agroforestry systems, and heterogeneous agricultural mosaics, can sustain substantial biodiversity by providing critical supplementary resources and acting as conduits for dispersal (Daily et al. 2003, Prevedello and Vieira 2010, Watling et al. 2011, Ferreira et al. 2018). Indeed, such permeable, high-quality matrices often reduce edge effects, mitigate extinction thresholds, and sustain viable populations even when habitat patches fall below sizes typically required in landscapes dominated by intensive agriculture or urbanization (Perfecto and Vandermeer 2008, Mendenhall et al. 2014, Boesing et al. 2018).

Despite these theoretical and empirical advances, existing conservation frameworks—such as the Key Biodiversity Area (KBA) approach (IUCN 2016) and the Aichi Biodiversity Targets (CBD 2010)—continue to overlook the matrix, often underestimating its potential contributions to biodiversity conservation (Prugh et al. 2008, Franklin and Lindenmayer 2009, Driscoll et al. 2013, Watson et al. 2018a, Kennedy et al. 2019, Galán-Acedo et al. 2019, Arroyo-Rodríguez et al. 2020, Fletcher et al. 2024). This persistent oversight highlights an urgent need for comprehensive global-scale research explicitly evaluating the ecological roles and conservation potential of matrix areas.

Overall, my findings contribute to our understanding of the conservation potential of the matrix for terrestrial mammals globally. Specifically, my research provides evidence that the condition of the matrix can mitigate the impacts of habitat fragmentation on extinction risk. Additionally, by comparing alternative conceptual models of habitat intactness, my work provides practical guidance on selecting models that more accurately characterize the relationship between habitat condition and extinction risk. Finally, by identifying areas within the matrix harboring high levels of species richness, my research underscores conservation opportunities that exist beyond primary habitats. Collectively, these findings contribute to a growing body of evidence highlighting the need to explicitly recognize and integrate the matrix into global biodiversity frameworks and management strategies. Such integration could strengthen conservation efforts by better supporting the persistence of terrestrial mammal species across human-modified landscapes.

To fully situate these objectives within the broader context of this research, the following subsections clarify the rationale for focusing on terrestrial mammals and outline the conceptual framework used to define and operationalize both habitat and the matrix throughout this dissertation.

Research objectives

In this dissertation, I evaluate the ecological role and conservation value of the matrix for terrestrial mammals on a global scale. Specifically, my research aims to:

1. Quantify how the matrix condition influences the effects of habitat fragmentation on extinction risk in terrestrial mammals.
2. Compare the predictive performance of alternative conceptual models of habitat intactness (patch-matrix, continuum, and hybrid models) for assessing extinction risk in terrestrial mammals.
3. Map global patterns of terrestrial mammal species richness within the matrix to identify conservation opportunities beyond primary habitats.

Overall, my findings contribute to our understanding of the conservation potential of the matrix for terrestrial mammals globally. Specifically, my research provides evidence that the condition of the matrix can mitigate the impacts of habitat fragmentation on extinction risk. Additionally, by comparing alternative conceptual models of habitat intactness, my work provides practical guidance on selecting models that more accurately characterize the relationship between habitat condition and extinction risk. Finally, by identifying areas within the matrix harboring high levels of species richness, my research underscores conservation opportunities that exist beyond primary habitats. Collectively, these findings contribute to a growing body of evidence highlighting the need to explicitly recognize and integrate the matrix into global biodiversity frameworks and management strategies. Such integration could strengthen conservation efforts by better supporting the persistence of terrestrial mammal species across human-modified landscapes.

To fully situate these objectives within the broader context of this research, the following subsections clarify the rationale for focusing on terrestrial mammals and outline the conceptual framework used to define and operationalize both habitat and the matrix throughout this dissertation.

Why focus on terrestrial mammals?

In light of their ecological roles, conservation concerns, and ongoing declines, terrestrial mammals represent a compelling focal group for global biodiversity assessments (Ceballos and Ehrlich 2002, Cardillo et al. 2005, Ripple et al. 2014). Beyond their ecological and conservation significance, the decision to center this research on terrestrial mammals was also shaped by practical considerations. At the time this work was initiated, they were the only vertebrate group for which globally consistent, high-resolution habitat data were available (Rondinini et al. 2011). These data offered the spatial resolution, taxonomic coverage, and global consistency required to develop the large-scale analyses presented in Chapter 2 of this dissertation. Although comparable high-resolution datasets are now available for birds (Lumbierres et al. 2022b), this study was designed to take advantage of the best available data at the time.

Conceptual definition of habitat

In this dissertation, habitat refers to the set of resources and conditions that support occupancy and, arguably, demographic performance (survival and reproduction) of a given species (Hall et al. 1997, Krausman and Morrison 2016). Habitat quality refers to the capacity of an environment to support persistence and should ideally be inferred from demographic evidence rather than species presence alone. Although habitat is often conceptualized along a continuum of suitability (Fischer and Lindenmayer 2006), the global-scale analyses in this work required simplifying this gradient into binary classes of “suitable” and “unsuitable” habitat, as defined by globally consistent habitat suitability models or Area of Habitat (AOH) maps (Rondinini et al. 2011, Brooks et al. 2019, Lumbierres et al. 2022b). This binary representation enabled tractable, comparable assessments across thousands of species while recognizing that areas classified as “unsuitable” may still provide important ecological functions.

In addition, habitat, as defined here in a species-specific sense, emerges from both abiotic conditions and biotic interactions (Morris 2003, Soberón 2007). Predation, competition, disease dynamics, and mutualisms can strongly shape realized habitat and demographic performance, including via trophic cascades (Paine 1969, Schmitz et al. 2000) and interaction-mediated edge effects (Ries et al. 2004). While these processes are central to many local and regional systems, they cannot be mapped consistently and comparably for thousands of species at a global scale. Consequently, the AOH maps applied in Chapters 2 and 4, together with the habitat intactness models developed in Chapter 3, provide standardized and defensible proxies for habitat condition but do not explicitly encode interspecific interactions—processes that have been shown to profoundly influence habitat structure and ecosystem function (e.g., Terborgh et al. 2001, Estes et al. 2011, Ripple et al. 2017).

Conceptual definition of the matrix

In this dissertation, the matrix refers to the land surrounding suitable habitat patches, regardless of ecological quality or degree of human modification. While much of the fragmentation literature conceptualizes the matrix as human-modified land that may hinder movement or reduce suitability (e.g., Fahrig 2003, Haddad et al. 2015, Wilson et al. 2016), matrix areas can also be entirely natural and undisturbed and, for some species, may provide suitable habitat (Prugh et al. 2008, Prevedello and Vieira 2010, Galán-Acedo et al. 2019). For example, in the Brazilian Cerrado, forested gallery patches occur within a natural savanna matrix (Oliveira-Filho and Ratter 2002). Although the savanna matrix differs ecologically from the forest patches, it can serve as primary habitat for savanna-adapted species while simultaneously influencing the persistence and movement of forest-dependent species. In this study, the operational focus on terrestrial mammal distributions naturally emphasizes land-based matrices, many of which are human-modified. However, this framing does not exclude the broader ecological definition in which matrix encompasses any non-focal land-cover type that influences species persistence and movement.

Dissertation structure

The chapters that follow this introduction (Chapters 2–4) are structured as standalone manuscripts intended for publication in peer-reviewed journals. Accordingly, these chapters are written in the first-person plural to acknowledge the contributions of my collaborators. A version of Chapter 2 has been published in *Nature Communications*, with M. Di Marco, J.E.M. Watson, C.J. Johnson, C. Rondinini, X. Corredor Llano, M. Arias, and O. Venter as co-authors (Ramírez-Delgado et al. 2022). A version of chapter 3 has been accepted for publication in *Ecography*, with M. Di Marco, C.J. Johnson, J.E.M. Watson, H.L. Beyer, L. de Assis Barros, R. Pillay, and O. Venter as co-authors (Ramírez-Delgado et al. in press). A version of chapter 4 has been prepared for submission, with M. Di Marco, J.E.M. Watson, C.J. Johnson, and O. Venter as co-authors (Ramírez-Delgado et al. in prep.). In the concluding chapter, I synthesize the key insights from these chapters and discuss their broader implications for conservation and future research.

Chapter 2: Matrix condition mediates the effects of habitat fragmentation on species extinction risk

Abstract

Habitat loss is the leading cause of the global decline in biodiversity, but the influence of human pressure within the matrix surrounding habitat fragments remains poorly understood. Here, we measure the relationship between fragmentation (the degree of fragmentation and the degree of patch isolation), matrix condition (measured as the extent of high human footprint levels), and the change in extinction risk of 4,426 terrestrial mammals. We find that the degree of fragmentation is strongly associated with changes in extinction risk, with higher predictive importance than life-history traits and human pressure variables. Importantly, we discover that fragmentation and the matrix condition are stronger predictors of risk than habitat loss and habitat amount. Moreover, the importance of fragmentation increases with an increasing deterioration of the matrix condition. These findings suggest that restoration of the habitat matrix may be an important conservation action for mitigating the negative effects of fragmentation on biodiversity.

Introduction

Although habitat loss is the leading cause of the ongoing biodiversity crisis (Newbold et al. 2015, 2016, Maxwell et al. 2016, Betts et al. 2017), the degree to which habitat fragmentation, defined as the spatial arrangement of remaining habitat for a given amount of habitat loss, influences the loss of biodiversity has remained the focus of considerable debate (Haddad et al. 2015, Fahrig 2017, 2019, Fletcher et al. 2018, Fahrig et al. 2019, Miller-Rushing et al. 2019). Central to the debate has been a persistent uncertainty in disentangling the effects of habitat loss on biodiversity from the effects of fragmentation *per se*, especially relative to the reduction in patch size and the increase in patch isolation (Fahrig 2003, 2019). While some studies have challenged the assumption of the impacts of fragmentation (Fahrig 2013, 2017, 2019, Fahrig et al. 2019), others have demonstrated that the effects of fragmentation are negative and stronger for local species (Hanski 2015, Haddad et al. 2015, Pfeifer et al. 2017, Fletcher et al. 2018), particularly in the tropics (Betts et al. 2019) and at intermediate (30–60%) levels of habitat amount (Pardini et al. 2010, Villard and Metzger 2014). Resolving this debate is critical to not just informing efforts to prioritize the protection and management of intact and fragmented landscapes with the same total amount of habitat, but also to better understand the role of the areas surrounding patches of habitat, commonly referred to as 'the matrix', in maintaining biodiversity (Prugh et al. 2008, Franklin and Lindenmayer 2009, Miller-Rushing et al. 2019).

The traditional characterization of landscapes, which views patches of habitat as islands embedded in a matrix of 'non-habitat', as assumed in classical theoretical models (MacArthur and Wilson 1967, Haila 2002), has been strongly criticized (Watson 2002, Watson et al. 2005, Prugh et al. 2008, Mendenhall et al. 2014). This characterization has progressively been relaxed with approaches based on the premise that the matrix should be treated as a heterogeneous mosaic of different land covers (e.g., 'countryside biogeography' (Daily et al. 2003), and the 'land-sharing' and 'land-sparing' approaches (Green et al. 2005, Perfecto and Vandermeer 2008, Law and Wilson 2015, Phalan 2018, Balmford et al. 2019)), as it is recognized that species use different matrices for foraging, dispersing, and reproduction purposes (Prevedello and Vieira 2010, Ferreira et al. 2018). While high-contrast matrices (e.g., intensive agricultural or built environments) act as movement barriers or ecological traps with an elevated risk of mortality for many species (Battin 2004), low-contrast matrices (e.g., secondary forests or shade-grown low-intensive agriculture in forested regions) may act as permeable barriers with a reduced risk of mortality for many others, even for those typically considered as habitat specialists (Daily et al. 2003, Perfecto and Vandermeer 2008). To date, however, conservation and management assessments have focused mainly on species' primary habitat (Martin et al. 2012, Di Marco et al. 2019), limiting our understanding of their response to the habitat matrix, which may have direct implications for the design of functional landscapes (Fahrig et al. 2011) and the prioritization of conservation actions in fragmented landscapes (Arroyo-Rodríguez et al. 2020).

Comparative extinction risk modelling is an approach for assessing the drivers of extinction risk and the change in risk over time. These models are based on the relationship between species' life histories, the habitat pressures within species' geographic ranges, and their threat status (Purvis et al. 2000, Fisher et al. 2003, Cardillo et al. 2005, Davidson et al. 2009, Di Marco et al. 2015, 2018b). Built with readily available data, this approach allows for the prediction of the risk of extinction of a larger number of species compared with that provided by expert-based assessments. This more rapid approach can substantially reduce resource requirements, as well as proactively inform conservation and management strategies (Rondinini et al. 2014, Bland et al. 2015a). However, despite the fact that the loss and fragmentation of habitat are among the main determinants of species extinction risk (Maxwell et al. 2016, Crooks et al. 2017, Di Marco et al. 2018b, Lucas et al. 2019), the influence of the matrix condition on the effects of fragmentation and its relationship with the risk of extinction has not been well evaluated for any animal taxon at a global scale.

Here, we quantify the relationship between changes in the extinction risk of 4,426 terrestrial mammals over a 24-year period (1996-2020), the fragmentation of their suitable habitat (in terms of the degree of fragmentation and the degree of patch isolation), and the levels of human pressure within the associated habitat matrix. Our goal is to test the influence of human pressure within the matrix on the effects of fragmentation for determining changes in species extinction risk globally. We focus on terrestrial mammals as they have been used as a focal taxon in previous extinction risk analyses (Arregoitia 2016), they are known to be sensitive to fragmentation (Crooks et al. 2017), and data are available to delineate levels of suitable habitat (i.e., high and medium habitat suitability) and unsuitable habitat (i.e., the matrix) within their ranges (Rondinini et al. 2011). For each species, we quantify the degree of fragmentation as the average Euclidean distance into 'core' suitable habitat from the nearest patch edge, the degree of patch isolation as the average Euclidean distance between patches of suitable habitat through the surrounding matrix, and the matrix condition as the extent of high human pressure levels overlapping with areas of unsuitable habitat. Spatial data representing the condition of the matrix were obtained from the recently updated human footprint maps (Venter et al. 2016, Williams et al. 2020), which provide a single metric of the combined area and intensity of human activities, all of which are driving the current biodiversity crisis (Maxwell et al. 2016). We define a human footprint threshold of ≥ 3 out of 50 to represent the extent of human-modified habitat within the matrix. This threshold was used as it has been shown to be the strongest predictor of transitions in extinction risk for terrestrial mammals (Di Marco et al. 2018b). Furthermore, this human footprint threshold is associated with the highest declines in mammalian movements (Tucker et al. 2018). Following previous studies (Hoffmann et al. 2010, Di Marco et al. 2015, 2018b), we classify species into two groups of extinction risk, 'low-risk' transitions and 'high-risk' transitions, based on the first and last Red List category registered between 1996 and 2020. In combination with other predictors of extinction risk (see Methods, Table 2.1), we quantify the relative importance of the degree of fragmentation, the degree of patch isolation, and the condition of the matrix for determining extinction risk transitions in terrestrial mammals.

Our analyses reveal that the condition of the matrix plays a major role on the effects of fragmentation for predicting extinction risk transitions in terrestrial mammals. Our results suggest that the negative effects of fragmentation may be somewhat mitigated when the matrix is associated with lower levels of human pressure.

Methods

Habitat suitability models

We used habitat suitability models developed by Rondinini et al. (2011) to represent the extent of suitable habitat patches and the extent of the matrix of 4,426 out of 5,709 extant terrestrial mammals, corresponding to ~78% of all species in the group (IUCN 2021). The models were limited to occur within the known geographic range of each species (i.e., the current "limits of distribution of a species, accounting for all known, inferred or projected sites of occurrence", as defined by the IUCN Red List of Threatened Species (IUCN 2016)), and built for the year 2000 at a spatial resolution of 300 m based on species' elevation range and other habitat affinities, including preferred land cover types, tolerance to human impact, and relationship to water bodies. Species' elevation range was incorporated into the habitat suitability models when known and recorded in the IUCN Red List. Textual descriptions of other habitat affinities for each species, derived from the input of thousands of mammal experts belonging to more than 30 specialist groups of the IUCN Species Survival Commission (IUCN/SSC) (Schipper et al. 2008), were also extracted from the IUCN database and input as quantitative data into the habitat suitability models. The models ranked areas with three levels of habitat suitability: (i) high, representing primary habitat or preferred habitat where the species can persist; (ii) medium, representing secondary habitat where the species can occur but not persist without nearby high suitable habitat; and (iii) unsuitable, representing locations where the species is expected to occasionally or never be found. A subset of the models and their associated levels of habitat suitability were validated against available points of known species occurrences. Full details on the development of the models are available elsewhere (Rondinini et al. 2011).

When delineating the levels of habitat suitability for each species, small contiguous groups of pixels (< 4 adjacent pixels of the same level of habitat suitability) were removed and replaced with the pixel value of the largest and nearest group of pixels, based on eight neighboring pixels of the same class. This reduced the influence of isolated groups of pixels of the same level of habitat suitability, and improved the computational efficiency of the analysis, as also reported in other studies (Crooks et al. 2011, 2017).

For our analysis, we combined high and medium habitat suitability to represent the extent of suitable habitat patches, and used the level of unsuitable habitat to represent the extent of the matrix of each species. We also applied a different combination of the levels of habitat suitability when representing the extent of suitable habitat patches (high suitability instead of high and medium suitability combined) and the extent of the matrix (medium suitability and unsuitable combined instead of unsuitable habitat alone) of each species as a sensitivity analysis (see Sensitivity analysis section).

The degree of habitat fragmentation and the degree of patch isolation as predictors of extinction risk transitions

For each species, we measured the degree of habitat fragmentation by calculating the average Euclidean distance of all the pixels of suitable habitat from the nearest edge (Ripple et al. 1991), edges demarcated by the boundary between suitable and unsuitable habitat. Large values of the average Euclidean distance represented low degrees of habitat fragmentation, whereas small values represented high degrees of habitat fragmentation. Additionally, we calculated the average Euclidean distance between patches of suitable habitat through the surrounding matrix (i.e., the average Euclidean distance of all the pixels of unsuitable habitat from the nearest edge) to account for patch isolation (after Crooks et al. 2017). Here, large values of the average Euclidean distance represented high degrees of patch isolation, and small values represented low degrees of patch isolation. The average Euclidean distance was considered because this metric does not require a predetermined distance threshold of what constitutes an edge, accounts for different shapes of fragments and landscapes patterns and arrangements, accounts for the distribution of habitat area (Li and Archer 1997), is comparable across landscapes of different extents, and provides stable and readily interpretable information (Crooks et al. 2011). Moreover, average Euclidean distance has been shown to be singularly valuable in quantifying the relationship between habitat fragmentation and extinction risk of the world's terrestrial mammals (Crooks et al. 2017), which made it highly suitable for our analyses.

The matrix condition as a predictor of extinction risk transitions

Spatially explicit data on the condition of the matrix, as represented by the extent and change over time of high human pressure levels overlapping with the area of unsuitable habitat surrounding patches of suitable habitat (after Di Marco et al. 2018), was obtained from the recently updated global human footprint maps (Williams et al. 2020). These maps represent the most comprehensive global distribution of changing human pressure on the environment at 1 km resolution between 2000 and 2013, based on eight pressure layers (Venter et al. 2016): (i) built environments; (ii) intensive agriculture; (iii) pasture land; (iv) human population density; (v) night-time lights; (vi) roads; (vii) railways; and (viii) navigable waterways, all of which are driving the current extinction crisis (Maxwell et al. 2016). Each human footprint map provides a single pressure metric ranging from 0 to 50, where a value of 0 represents areas free of any human influence (e.g., terrestrial remaining wilderness), values of 4 or below represent areas of low human pressure (e.g., pasture lands), and values above 20 represent areas with very high pressure levels (e.g., densely populated semi-urban and urban environments).

In this analysis, we measured the extent of high human footprint values and the change of this extent over time (between 2000 and 2013) within areas of unsuitable habitat, using a defined human footprint threshold of 3 or above. This threshold was used as it has shown to be the strongest predictor of extinction risk transitions in terrestrial mammals (Di Marco et al. 2018b). Moreover, this human footprint threshold is associated with the highest declines in mammalian movements (Tucker et al. 2018). Based on previous studies (Di Marco et al. 2013, 2018b), we used the extent of high human footprint values within the matrix as the extent of high pressure levels within species' ranges has been shown to be more sensitive to predict extinction risk than using mean values of human pressure within species' ranges. We also considered the change in the extent of high human footprint values after discarding areas where the human footprint was lower in 2013 than in 2000 (assuming no change in these particular areas), as decreases in human pressure levels are likely to take time before having a measurable effect on species threat status, particularly for species with a long generation time period (Di Marco et al. 2018b).

Changes in species extinction risk

We used the IUCN Red List of Threatened Species (IUCN 2012, 2021), the retrospective Red List assessments published in Hoffmann et al. (2010), and the IUCN list of genuine changes in the conservation status of mammal species (https://www.iucnredlist.org/resources/summary-statistics) to represent trends in extinction risk of terrestrial mammals. Following the classification of extinction risk transitions developed by Di Marco et al. (2015, 2018), we classified the species into two main groups, 'low-risk' transitions and 'high-risk' transitions (Fig. 2.1). The low-risk group included species that retained a category of least concern, together with those species that moved from any higher category of threat to a lower category assessment period. The high-risk group included all species that retained a category of threatened or near threatened, together with those species that moved from any lower category of threat to a higher category over time.

For our analysis, we classified species into the two extinction risk groups (low-risk transitions and high-risk transitions) based on the first and last Red List category registered between 1996 and 2020. In order to test the sensitivity of this classification, we also classified all species into the two extinction risk groups based on the last two Red List assessments registered between 1996 and 2020 (i.e., the second to last and last Red List categories registered during this time period). With this classification, however, only two species (0.05% of 4,426 species in our sample) changed their extinction risk transition (from a high-risk transition to a low-risk transition) compared to that based on the first and last Red List category registered during the study period. We thus only reported the main results using the first and last Red List category registered between 1996 and 2020.

We excluded species without a defined level of habitat suitability, those not evaluated in the Red List, and those categorized as Data Deficient, Extinct and Extinct in the Wild in the last Red List assessment reported during the study period, as long as they have not shown a defined transition of extinction risk (see Fig. 2.1) along the study period.

Predicting extinction risk transitions

We used a multivariate Random Forest model to predict extinction risk transitions in terrestrial mammals (Fig. 2.1). Random Forest is a non-parametric, tree-based, machine-learning technique that produces multiple decision trees using a randomly selected subset of training samples and variables to make a prediction (Breiman 2001, Cutler et al. 2007). Due to its limited assumptions on data distributions, its high classification stability and performance, and its ability to cope well with a large number of potentially correlated predictors and non-linear responses, Random Forest is a highly suitable technique for species threat status classification (Murray et al. 2014). Furthermore, Random Forest modelling has demonstrated superior performance among several machine learning techniques tested for the prediction of global extinction risk of terrestrial mammals (Bland et al. 2015b), making it ideal for this study.

In this analysis, we optimized the number of trees to grow and the number of predictors sampled for splitting at each node from 3 repeats of 10-fold cross-validation, using 75% of the data as training data and 25% as test data. Predictors included: (i) the extent of high human footprint values in the matrix; (ii) the extent of high human footprint values in patches of suitable habitat; (iii) the change over time of high human footprint values in the matrix; (iv) the change over time of high human footprint values in patches of suitable habitat; (v) the degree of fragmentation of suitable habitat; (vi) the degree of isolation between patches of suitable habitat; (vii) the proportion of suitable habitat; and (viii) the biogeographic realm in which the species can be encountered (see Table 2.1 for a description). Because mammals of greater body size usually move farther (Jetz et al. 2004), and diet may influence their movements as a result of differences in availability of resource types and foraging cost (McNab 1986, Tucker et al. 2014), we decided to include body size and dietary breadth as life-history predictors. We also included the reproductive traits, weaning age, and gestation length. Other life-history traits were broadly captured by including taxonomic orders. Because the levels of habitat suitability are limited by the size of species' geographic ranges, we did not include species' range size as a predictor in order to avoid potential circularity in the estimation of extinction risk (Purvis et al. 2000).

Table 2.1: Description of the selected variables to predict extinction risk transitions in terrestrial mammals.

Class	Variable	Description	Source
Pressure	High human footprint extent in the matrix	Proportion of unsuitable habitat overlapping with high human footprint values in 2000.	Rondinini et al. 2011, Williams et al. 2020
	High human footprint extent in patches of suitable habitat	Proportion of suitable habitat overlapping with high human footprint values in 2000.	Rondinini et al. 2011, Williams et al. 2020

	High human footprint change in the matrix	Difference in the proportion overlap between the area of unsuitable habitat and high human footprint values during 2000 and 2013.	Rondinini et al. 2011, Williams et al. 2020
	High human footprint change in patches of suitable habitat	Difference in the proportion overlap between the area of suitable habitat and high human footprint values during 2000 and 2013.	Rondinini et al. 2011, Williams et al. 2020
Environment	Degree of habitat fragmentation	Average of the Euclidean distance from the edge to the 'core' (i.e., the interior) of each patch of suitable habitat.	Ripple et al. 1991, Rondinini et al. 2011
	Degree of patch isolation	Average of the Euclidean distance between patches of suitable habitat from the edge to the 'core' (i.e., the interior) of each area of unsuitable habitat.	Crooks et al. 2017
	Proportion of suitable habitat	Proportion of suitable habitat within the range of each species.	Rondinini et al. 2011

	Realm	Biogeographic realm in which the species can be encountered.	IUCN 2012, 2021
Life-history	Body mass	A generic proxy of species life history and energetic requirements.	Smith et al. 2003, Jones et al. 2009, Tacutu et al. 2013, Verde Arregoitia et al. 2013, Faurby et al. 2018
	Diet	Dietary categories: vertebrate carnivore (> 90% vertebrate matter ingested), invertebrate carnivore (> 90% invertebrate matter ingested), omnivore (10-90% animal matter ingested or 10-90% plant matter ingested), herbivore (> 90% plant matter ingested).	Kissling et al. 2014, Wilman et al. 2014, Faurby et al. 2018
	Weaning age	A proxy of species reproductive timing.	Jones et al. 2009, Tacutu et al. 2013
	Gestation length	A proxy of species reproductive output.	Jones et al. 2009, Tacutu et al. 2013
	Order	Species taxonomic order.	IUCN 2012

We measured the predictive importance of each variable using the mean decrease in classification accuracy (MDA) metric (Breiman 2001), which reports the model's ability to correctly classify data if the values of a predictor variable are randomly permuted. Based on this metric, we then calculated the relative importance of each variable using the model improvement ratio (MIR) metric (Murphy et al. 2010), which scales raw importance scores from 0 to 1. Unlike the raw importance scores, the MIR metric is not influenced by the total number of variables and is comparable among models. MIR is calculated as $[I_n/I_{max}]$, where I_n is the importance of a given variable, and I_{max} is the maximum model improvement score. We also reported the overall performance of the Random Forest model through cross-validation in terms of proportion of correctly classified species (accuracy), proportion of correctly classified high-risk species (sensitivity), proportion of correctly classified low-risk species (specificity), and the true skill statistic (TSS = sensitivity + specificity – 1) (Allouche et al. 2006).

Assessing the influence of the matrix on the importance of fragmentation for predicting extinction risk transitions

To measure the influence of the matrix condition on the importance of habitat fragmentation (in terms of the degree of fragmentation and the degree of patch isolation) for the prediction of extinction risk transitions, we first defined two broad levels of quality of the matrix, 'low-quality' matrices and 'high-quality' matrices, based on the proportion of high human footprint values within the matrix of each species. When delimiting the two levels of quality of the matrix, the extent of high human footprint values in the matrix of each species was discretized into two intervals based on the positive and negative effect that the matrix condition had on the probability of high-risk transitions (see Fig. 2.3c). We then built separate Random

Forest models for species restricted to such levels of quality of the matrix. Using the MDA metric (Breiman 2001) and the MIR metric (Murphy et al. 2010), we measured the relative importance of the degree of habitat fragmentation and the degree of patch isolation, including the other selected predictors of extinction risk (Table 2.1), from the built Random Forest models. We used cross-validated measures of accuracy, sensitivity, specificity, and the true skill statistic to evaluate the overall performance of the models (Allouche et al. 2006). We also used Wilcoxon rank sum tests to test for statistical differences in the degree of fragmentation and patch isolation between low-risk and high-risk species restricted to the defined levels of quality of the matrix. In order to determine the effect size of the degree of habitat fragmentation and patch isolation between low-risk and high-risk species for each of the levels of quality of the matrix, we used Cohen's d statistic (Cohen 1988).

Sensitivity analysis

To test the sensitivity of our model, we built additional Random Forest models based on a different combination of the levels of habitat suitability to represent the extent of suitable habitat patches (high suitability instead of high and medium suitability combined) and the extent of the matrix (medium suitability and unsuitable combined instead of unsuitable habitat alone). From these models, the relative importance of each variable was quantified using the MDA metric (Breiman 2001) and the MIR metric (Murphy et al. 2010). The overall performance of these models was reported through cross-validation in terms of accuracy, sensitivity, specificity, and the true skill statistic (Allouche et al. 2006).

All spatial analyses were performed in python using the ArcPy processing module from ArcGIS Pro 2.8.2 (ESRI 2021). Statistical analyses were performed in R (R Core Team 2021), using the packages ‘randomforest’ (Liaw and Wiener 2002), ‘caret’ (Kuhn 2008), ‘iml’ (Molnar and Schratz 2020), and ‘effsize’ (Torchiano 2017).

Results

Changes in species extinction risk

We found that 2,984 (67.4%) terrestrial mammals faced a low-risk transition and 1,442 (32.6%) a high-risk transition between 1996 and 2020 (Fig. 2.1). A total of 4,124 species (93.2%) retained the same Red List category, while 302 (6.82%) changed their category through time (Appendix A, Fig. A.1).

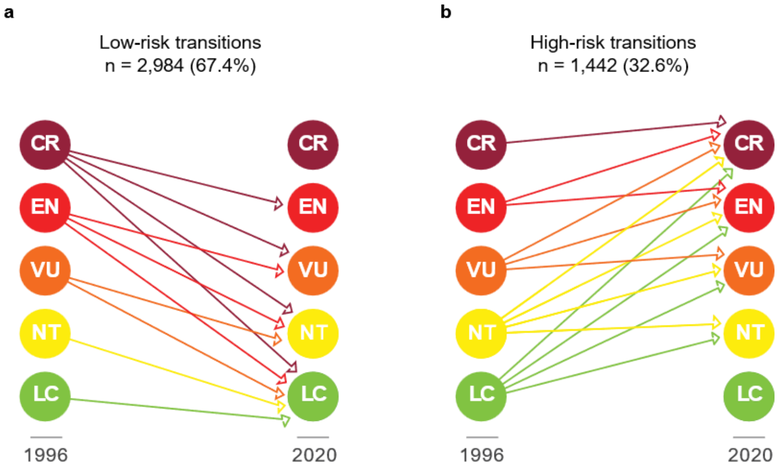

Figure 2.1: Classification of species extinction risk transitions based on past and present IUCN Red List categories. Low-risk transitions included species that retained a category of least concern, together with those species that moved from any higher category of threat to a lower category between 1996 and 2020 (a). High-risk transitions included all species that retained a category of threatened or near threatened, together with those species that moved from any lower category of threat to a higher category between 1996 and 2020 (b). Acronyms refer to the IUCN Red List categories, including Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR).

Predicting transitions in species extinction risk

We used a Random Forest model for classification (Breiman 2001) to measure the performance of an array of pressure, environmental and life-history variables (Table 2.1) for the prediction of extinction risk transitions in terrestrial mammals. We found that the degree of fragmentation of suitable habitat had higher predictive performance than species life-history traits, human pressure variables, and other environmental conditions (Fig. 2.2).

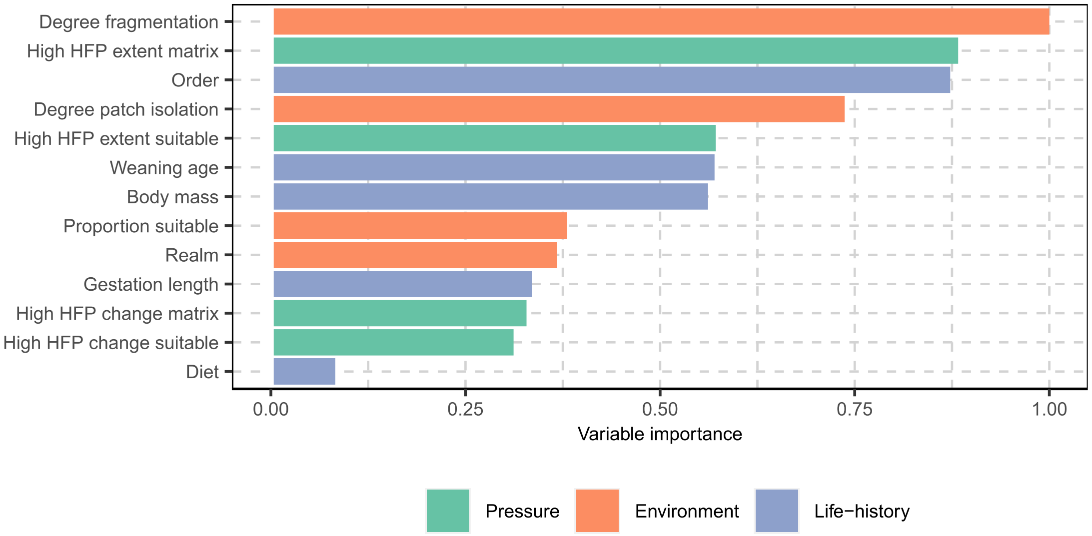

Figure 2.2: Relative importance of selected variables for the prediction of extinction risk transitions in terrestrial mammals. Variables are colour-coded according to their broad class (human pressure, environment, and life-history). The description of each variable can be found in Table 2.1. High levels of the human footprint (HFP) included values of 3 or above.

Interestingly, our results show that the degree of fragmentation, the extent of high human footprint values in the matrix, and the degree of patch isolation had higher predictive performance than the change in high human footprint values (as defined by increases in high human footprint values through time) within suitable habitat and the proportion of suitable habitat (Fig. 2.2). This result was supported by a sensitivity analysis where a different combination of the levels of habitat suitability was applied (Appendix A, Fig. A.2a,b). This suggests that habitat fragmentation and the matrix condition better predict changes in species extinction risk than habitat loss and habitat amount at a global scale.

Partial dependence plots show that the probability of high-risk transitions is higher with an increasing degree of fragmentation (Fig. 2.3a), a decreasing degree of patch isolation (Fig. 2.3b), and an extent of high human footprint values within the matrix of 100% (Fig. 2.3c).

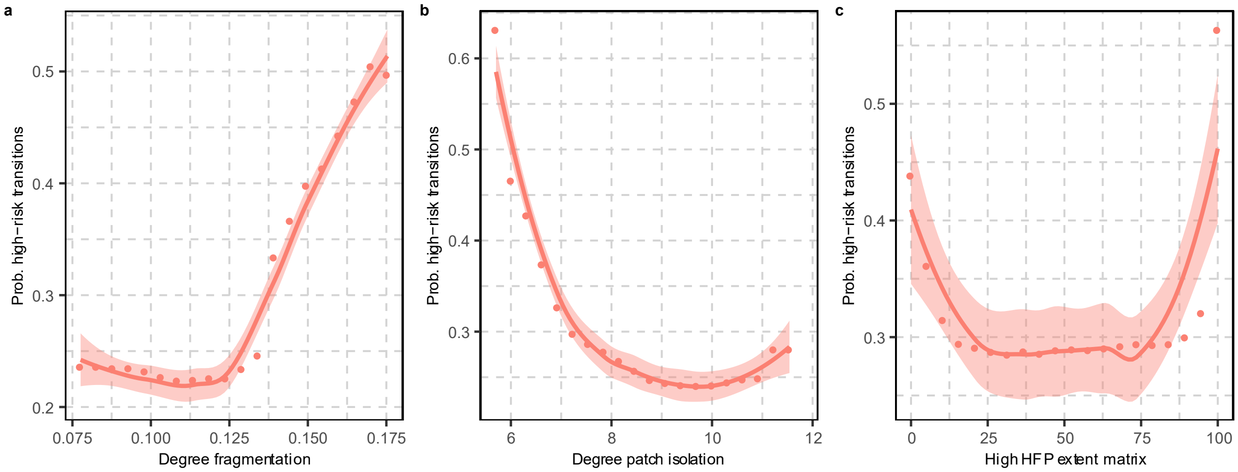

Figure 2.3: Partial dependence plots to show the effect of the degree of habitat fragmentation, the degree of patch isolation, and the matrix condition on extinction risk transitions in terrestrial mammals. The plots show the probability of high-risk transitions as a function of the degree of fragmentation (a), the degree of patch isolation (b), and the extent of high human footprint values within the matrix (c). Solid red lines and shading represent fitted LOESS curves and 95% credible intervals for the relationships between the probability of high-risk transitions and each explanatory variable. As partial dependence plots for Boolean response variables mirror each other, the probability of low-risk transitions as a function of these variables are not depicted in the figure. Values of the degree of fragmentation and the degree of patch

isolation were ln-transformed for visual purposes. The degree of fragmentation was inverse-coded so high values represent high degrees of fragmentation. High values of the degree of patch isolation represent high degrees of isolation between patches of suitable habitat. The description of each variable is given in Table 2.1. High levels of the human footprint (HFP) included values of 3 or above.

Our model showed good overall classification ability during cross-validation, with an accuracy of 81.2%. The proportion of correctly classified high-risk transitions (sensitivity = 60.5%) was lower than the proportion of correctly classified low-risk transitions (specificity = 90.9%), with a true skill statistic of 0.51.

The predictive performance of our model did not markedly change compared to the model built with a different combination of the levels of habitat suitability (Appendix A, Table A.1). Thus, the model is robust to changes in the levels of habitat suitability.

The influence of the matrix condition on the importance of habitat fragmentation for predicting extinction risk transitions

In order to measure the influence of the matrix condition on the importance of fragmentation (i.e., the degree of fragmentation and the degree of patch isolation) for the prediction of extinction risk transitions, we first discretized the extent of high human footprint values within the matrix of each species into two broad levels as a proxy for matrix quality: ‘low-quality’ matrices and ‘high-quality’ matrices. As the global distribution of the matrix condition showed to be uneven in both low-risk and high-risk species (Appendix A, Fig. A.3), even at the scale of individual biogeographic realms (Appendix A, Fig. A.4), we defined cutoff values for each of the levels of quality of the matrix based on the positive and negative effect that the matrix condition had on the probability of high-risk transitions (Fig. 2.3c). Low-quality matrices were therefore represented by species with extents > 84.2% of their matrix overlapping with high human footprint values (*n* = 1,815 low-risk species and 1,027 high-risk species), while high-quality matrices by those species with extents < 15.8% of their matrix overlapping with high human footprint values (*n* = 60 low-risk species and 29 high-risk species). We then built separate Random Forest models for each level of quality of the matrix in order to compare the relative importance of the degree of fragmentation of suitable habitat and the degree of isolation of patches of suitable habitat between species with a matrix of low-quality habitat and species with a matrix of high-quality habitat.

We found that the degree of fragmentation and the degree of patch isolation had higher relative importance for species with a low-quality matrix (Fig. 2.4a) than that observed for species with a high-quality matrix (Fig. 2.4b), with a decrease of 33.3% and 62.5%, respectively. Notably, the relative importance of the extent of high human footprint values in the matrix was markedly higher for those species with a low-quality matrix than for those with a high-quality matrix, with a decrease of 116.4%, suggesting that the lower the quality of the matrix, the higher the predictive importance of the matrix for predicting extinction risk transition in terrestrial mammals.

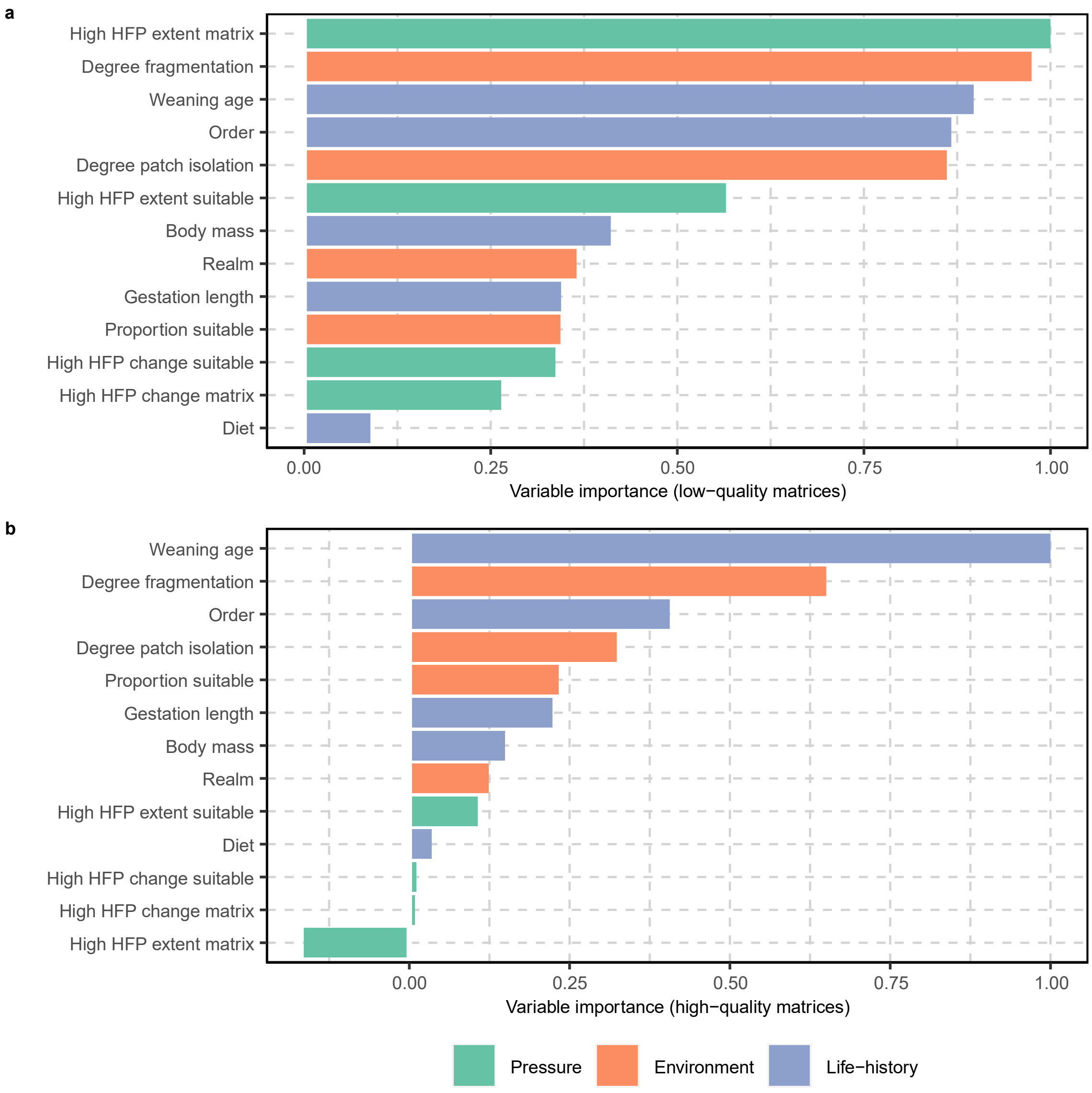

Figure 2.4: Influence of the matrix condition on the relative importance of selected variables for the prediction of extinction risk transitions in terrestrial mammals. Relative importance of each predictor for species with a low-quality matrix (a), which included proportions > 84.2% of the extent of their matrix overlapping with high human footprint values (*n* = 1,815 low-risk species and 1,027 high-risk species). Relative importance of each predictor for species with a high-quality matrix (b), which included proportions < 15.8% of the extent of their matrix overlapping with high human footprint values (*n* = 60 low-risk species and 29 high-

risk species). Variables are colour-coded according to their broad class (human pressure, environment, and life-history). The description of each variable is given in Table 2.1. High levels of the human footprint (HFP) included values of 3 or above.

When looking at the difference in the degree of fragmentation and the degree of patch isolation between low-risk and high-risk species with a low-quality matrix, we found that both variables were significantly higher for those species classified as high-risk (*p*-values < 0.001; Wilcoxon rank sum test, one-sided). We also found that the difference in the degree of fragmentation and the degree of patch isolation between low-risk and high-risk species with a high-quality matrix was not statistically significant (*p*-values > 0.05; Wilcoxon rank sum test, one-sided). The degree of fragmentation and the degree of patch isolation showed a greater effect size between low-risk and high-risk species with a matrix of low-quality habitat, with an estimated Cohen's d of 0.23 and 0.32, respectively (Appendix A, Fig. A.5a,b). This indicates a greater effect of both the degree of fragmentation and the degree of isolation between patches of suitable habitat on the risk of extinction of those terrestrial mammals with a matrix of low-quality habitat.

Our results show that the model for species with a matrix of low-quality habitat had higher predictive performance (true skill statistic = 0.57) than the model for species with a matrix of high-quality habitat (true skill statistic = 0.36). Our results also show that the classification ability was higher in the model for species with a low-quality matrix (accuracy = 0.81) compared to that shown in the model for species with a high-quality matrix (accuracy = 0.76). Although the proportion of correctly classified high-risk transitions was higher in the model for species with a low-quality matrix (sensitivity = 68.4%), relative to that shown in the model for species with a high-quality matrix (sensitivity = 42.9%), the model for species with a low-quality matrix had a lower proportion of correctly classified low-risk transitions (specificity = 88.7%) than the model for species with a high-quality matrix (specificity = 92.9%). This indicates a higher imbalance between the proportion of low-risk species and high-risk species correctly classified in the model for species with a high-quality matrix.

Discussion

Understanding the external conditions under which a species is likely to face an increased risk of extinction are necessary to inform conservation policies and management strategies (Di Marco et al. 2015). We found that the condition of the matrix, as defined by the extent of high human footprint values between patches of suitable habitat, strongly influenced the effects of fragmentation on extinction risk transitions of terrestrial mammals. Specifically, we found that the degree of fragmentation and the degree of patch isolation had a higher relative importance for species with a matrix of low-quality habitat compared to those with a matrix of high-quality habitat when determining extinction risk transitions in terrestrial mammals. To the best of our knowledge, these findings are the first to demonstrate the extent to which human pressure within the matrix alters the importance of fragmentation metrics as predictors of extinction risk transitions in terrestrial mammals. These findings are in line with previous studies showing that the use of the matrix is among the main determinants of the vulnerability of mammalian populations to local extinction in fragmented landscapes (e.g., Laurance 1991, Daily et al. 2003, Viveiros de Castro and Fernandez 2004), and support recent findings showing that species-area relationships are steeper (i.e., more extinction driven) in forested landscapes with a low-quality matrix, and shallower (i.e., less extinction driven) in those forested landscapes with a higher quality matrix (Reider et al. 2018). This suggests that the magnitude of the effects of fragmentation depends on the structural similarity between suitable habitat patches and the matrix, as also suggested by a growing body of evidence across multiple taxa on a local scale (Ewers and Didham 2006, Prevedello and Vieira 2010).

Our results showed that species with a greater degree of fragmentation, a lower degree of patch isolation, and a lower quality matrix within their ranges tended to be at greater risk of extinction. This indicates that the persistence of terrestrial mammals depends not only on the proportion of suitable habitat and its spatial configuration, but also on the quality of the matrix. This pattern may reflect the fact that species occurring in regions with low rates of historical disturbance are more likely to be sensitive to fragmentation (Betts et al. 2019), and thus more likely to face an increased risk of extinction. That would suggest that those species within the high-risk group are mainly concentrated in the tropics, particularly in forested landscapes where deforestation continues at a rapid rate (Schipper et al. 2008, Tracewski et al. 2016). In our sample, the majority of these species (68.4%) were restricted to the Neotropical (32.0%), Afrotropical (34.9%), and Indo-Malay (48.0%) biogeographic realms, which is consistent with these findings.

In our global analysis, the degree of patch isolation refers to the average Euclidean distance between patches of suitable habitat across a species' entire range, rather than local dispersal distances within a single landscape. High isolation values can indicate widely separated patches—sometimes occurring on different continents—rather than fragmentation of a continuous habitat. The loss of any single patch does not necessarily elevate extinction risk if other distant patches remain intact. While local-scale studies consistently show that greater isolation between patches reduces colonization, limits gene flow, and increases extinction probability (Fahrig 2003, Haddad et al. 2015), larger-scale research reveals more complex, scale-dependent patterns. For example, variation in the arrangement of habitat patches across broad areas can enhance regional diversity (Perrin et al. 2025), and networks of small but widely distributed patches may support higher species richness even when total habitat area remains the same (Riva and Fahrig 2023). Our finding—that high-risk transitions decreased with increasing patch isolation—should therefore be seen as a global-scale effect, where broad geographic separation between patches can buffer species against synchronized threats, rather than as evidence that isolation is beneficial at local scales.

In our extinction risk model, some variables had higher predictive performance than others. For example, the degree of fragmentation of suitable habitat was shown to be the most important predictor of changes in species extinction risk when compared with species life-history traits, measures of human pressure, and other environmental conditions. This finding is in line with previous extinction risk modelling, showing that the inclusion of the degree of fragmentation as a predictor increases the explanatory power of the models (Crooks et al. 2017, Lucas et al. 2019). In particular, this result supports recent findings showing that terrestrial mammals with a higher degree of fragmentation have smaller ranges, lower proportions of suitable habitat, and are at greater risk of extinction (Crooks et al. 2017).

The second most important predictor of extinction risk transitions was the extent of high human footprint values within the matrix (i.e., the condition of the matrix). This result contrasts with the findings from previous extinction risk modelling exercises for mammals, where the predictive importance of human pressure was found to be lower than life-history traits or environmental conditions different from fragmentation (Cardillo et al. 2008, Murray et al. 2014, Arregoitia 2016). However, it complements the findings of one recent extinction risk modelling exercise for mammals (Di Marco et al. 2018b), where the extent of high human footprint values within species' ranges had higher predictive importance than species life-history traits, environmental conditions (without consideration of habitat fragmentation), and other pressure variables. Given that species are not homogeneously distributed throughout their ranges (Rondinini et al. 2006, 2011), this result specifically suggests that the condition of the matrix surrounding patches of suitable habitat is strongly correlated with extinction risk transitions in terrestrial mammals. This may in part be explained by the fact that habitat loss and fragmentation have opened up the path to a series of other threat mechanisms through the matrix, such as hunting, disease spread, and invasive species (Cardillo et al. 2005, Haddad et al. 2015, Betts et al. 2017). It may also be related to the fact that species are increasingly obligated to inhabit human-modified landscapes (Watling et al. 2011, Galán-Acedo et al. 2019), many of which have a matrix that likely prevents their movement (Tucker et al. 2018) and elevates their mortality (Battin 2004) (e.g., by roadkill (Fahrig and Rytwinski 2009) or increasing predation (May and Norton 1996, Woinarski et al. 2015)).

Conflicting results on the effects of fragmentation on biodiversity have arisen from studies attempting to separate 'independent' effects of habitat loss from those of habitat fragmentation (Fahrig 2003). Some studies have argued that the effects of habitat loss are greater and more negative (e.g., Fahrig 2013, 2017, 2019, Fahrig et al. 2019), while others have demonstrated that the effects due to fragmentation (such as declining patch size, increasing habitat isolation, and increasing edge effects) are essentially negative and lasting (e.g., Hanski 2015, Haddad et al. 2015, Pfeifer et al. 2017, Fletcher et al. 2018). However, in real landscapes, habitat loss inevitably causes habitat fragmentation, and both act in synergy with other threats to biodiversity (Peres 2001, Laurance and Useche 2009, Côté et al. 2016). Thus, there is little practical value in attempting to separate the effects of habitat loss and fragmentation (Didham et al. 2012, Ruffell et al. 2016, Morante-Filho et al. 2018, Fletcher et al. 2018). Our study does not attempt to resolve the current debate as to whether and how habitat fragmentation *per se* (i.e., the spatial arrangement of remaining habitat for a given amount of habitat loss) influences biodiversity (Haddad et al. 2015, Fahrig 2017, 2019, Fletcher et al. 2018, Fahrig et al. 2019, Miller-Rushing et al. 2019), but our results showed that the degree of fragmentation of suitable habitat, the extent of high human footprint values within the matrix, and the degree of isolation between patches of suitable habitat were more important predictors of extinction risk transitions than the change in high human footprint values (as represented by increases in high human pressure levels over time) within patches of suitable habitat and the proportion of suitable habitat. This suggests that changes in species extinction risk are primarily determined by the fragmentation of habitat and the matrix condition, and secondarily by the loss and the amount of habitat within species' ranges. However, there is also the possibility that the loss of most suitable habitat patches had already occurred before the beginning of the study period, resulting in the degree of fragmentation, the matrix condition, and the degree of patch isolation being more important predictors of extinction risk than habitat loss and habitat amount.

Although biogeography was not a key parameter for determining extinction risk transitions in our models, we found some differences in the way the matrix condition was distributed in low-risk and high-risk species among biogeographic realms. The Indo-Malay realm represented a particular case, with a highly left-skewed distribution (i.e., towards a higher extent of high human footprint values within the matrix) in species classified as low-risk, very similar to that shown in high-risk species. With ~87% of terrestrial mammals showing a low-quality matrix in the Indo-Malayan realm, this might indicate that species living in the Indo-Malayan realm are relatively more resilient to those human activities included in the human footprint, but more vulnerable to other threats (such as overexploitation, relevant in Southeast Asia (Sodhi et al. 2004)), as also suggested by others (Di Marco et al. 2018b). The Australasia realm also represented a particular case, with an approximately bimodal distribution of the matrix condition in low-risk species and a less right-skewed distribution in those classified as high-risk relative to that shown in other realms. Interestingly, the Australasia realm showed a lower proportion of species with a low-quality matrix (37.7%) when compared to other realms, suggesting that species restricted to this realm have relatively lower levels of human activity within their matrix. This is perhaps unsurprising given the fact that most recent declines of Australian terrestrial mammals have occurred in areas with low human population pressures, where native vegetation has not been significantly removed, particularly in the interior deserts and tropical savannas (Woinarski et al. 2015). In fact, the decline of most Australian species has been directly related to predation by introduced species (such as the feral cat, *Felis catus*, and the red fox, *Vulpes vulpes*) and changes in fire regimes (May and Norton 1996, Woinarski et al. 2015), which are not included in the human footprint.

Our models were better at correctly classifying low-risk transitions than high-risk transitions. This suggests that the external conditions leading to a high-risk transition might be more difficult to identify than those leading to a low-risk transition, as also indicated in previous studies (Davidson et al. 2009, Murray et al. 2014, Bland et al. 2015b, Di Marco et al. 2015, 2018b). However, it is important to acknowledge that the exclusion of other variables associated with pressure (such as overhunting, disease, invasive species, and climate change) and life-history traits (such as rarity, dispersal mode, and ranging behavior) could have increased the uncertainty of our predictions, and thus influenced the ability of our models to correctly classify high-risk transitions.

An important next step will be to create a global map by weighting the extent of the matrix of the world's terrestrial mammals with the human footprint in order to highlight those matrix habitats with a high number of species and low human pressure levels, and those with a high number of species and high human pressure levels. If species threat statuses are considered, such an analysis could have the potential to identify where conservation actions need to be improved. For example, in those locations where species with an increased risk of extinction show a low-quality habitat within their matrix, a land-sparing approach could be effective as it maximizes conservation actions on the remaining patches of suitable habitat while concentrating agricultural production elsewhere (Green et al. 2005, Law and Wilson 2015, Phalan 2018, Balmford et al. 2019). Alternatively, in those locations where species with an increased risk of extinction show a high-quality habitat within their matrix, a land-sharing approach would work better as it minimizes the impact of agricultural production by maintaining or restoring the conservation value of the land already farmed (Perfecto and Vandermeer 2008, Law and Wilson 2015, Phalan 2018, Balmford et al. 2019).

Our results indicate that species suffering from greater pressure in their matrix require particular conservation attention. Among these species, those with smaller ranges require careful management of the areas surrounding their suitable habitat, especially in light of the current and future effects of climate and land-use change (Segan et al. 2016). Our results also highlight the potential of high-quality matrices to mitigate the negative effects of fragmentation on species extinction risk, thus suggesting that in addition to efforts to maintain remaining suitable hábitat

(Ferreira et al. 2018, Maron et al. 2018, Di Marco et al. 2019), there is a need for restoration of habitats in the matrix.

Chapter 3: Global comparison of habitat intactness models for predicting extinction risk in terrestrial mammals

Abstract

The effects of habitat condition on biodiversity are primarily investigated using discrete (patch-matrix) habitat models that consider habitat fragments as islands embedded in an inhospitable matrix. Recently, continuum habitat models, which focus on ecological gradients without defining habitat or matrix, have emerged. However, no formal comparison between patch-matrix, continuum, and hybrid habitat models (which combine characteristics of both) has been undertaken globally. Here, we compare the ability of patch-matrix, continuum, and hybrid models of habitat intactness to explain the risk of extinction for terrestrial mammals on a global scale. We discover that hybrid models outperform both patch-matrix and continuum models of habitat intactness in predicting extinction risk, regardless of a species' habitat specialization. Moreover, we find that the magnitude of the relationship between habitat intactness and the predicted probability of a species being threatened is stronger when employing hybrid habitat models. Our results suggest that combining a patch-matrix designation with a continuous representation of habitat condition can improve extinction risk analyses and provide valuable insights for conservation efforts.

Introduction

The traditional characterization of habitat, which views habitat patches as islands embedded in a matrix of non-habitat, has shaped how habitat condition has been assessed over the past five decades (Ricketts 2001, Watson et al. 2005, Laurance 2008). This binary representation of habitat, commonly referred to as the patch-matrix model, has progressively been relaxed with the emergence of new approaches (e.g., Daily et al. 2001, 2003, Green et al. 2005) that recognize the potential of the matrix to provide resources, refugia, and microclimatic conditions for sustaining biodiversity (Fischer and Lindenmayer 2007). Rather than defining habitat as isolated patches surrounded by an inhospitable matrix, the continuum model represents habitat as a gradient of ecological conditions with varying levels of suitability and connectivity (Fischer and Lindenmayer 2007, Brudvig et al. 2017). However, despite the argument that combining characteristics of patch-matrix and continuum models to represent habitat—often referred to as hybrid models—can better explain species diversity and abundance (Price et al. 2009), formal comparisons between patch-matrix, continuum, and hybrid habitat models remain largely unexplored (Brudvig et al. 2017).

Species vary in their sensitivity to habitat degradation, and understanding how different representations of habitat intactness capture extinction risk is critical for effective conservation planning (Henle et al. 2004, Ewers and Didham 2006). Habitat condition—including both its current state and recent degradation—is increasingly recognized as a key determinant of species persistence (e.g., Fahrig 2001, Betts et al. 2017). Yet no study has systematically compared patch-matrix, continuum, and hybrid representations of habitat intactness in their ability to explain extinction risk for any animal taxon at a global scale.

Here, we compare the ability of patch-matrix, continuum, and hybrid models of habitat intactness, defined as the degree or extent to which a species' range remains free of human activities or significant human alterations, to predict the risk of extinction for terrestrial mammal species globally. We focus our analysis on terrestrial mammals as they are known to be sensitive to habitat conditions (Crooks et al. 2017, Ramírez-Delgado et al. 2022) and have often served as a focal taxon in extinction risk analyses (Arregoitia 2016). We classified species as 'habitat generalists' or 'habitat specialists' to recognize that specialized species are particularly vulnerable to intactness given their discontinuous distributions, reduced local abundance, and sensitivities to anthropogenic disturbances (McKinney and Lockwood 1999, Henle et al. 2004, Charrette et al. 2006, Devictor et al. 2008). We expected patch-matrix models to outperform continuum models in predicting extinction risk for habitat specialists because their food and other resources are often patchy in space and time (Devictor et al. 2008, Arroyo-Rodríguez et al. 2020). Conversely, we expected that continuum models would be better than patch-matrix models at predicting extinction risk for habitat generalists because of their propensity to use a broader range of habitat types (McKinney and Lockwood 1999, Henle et al. 2004, Devictor et al. 2008). Given that hybrid models standardize data inputs across the two model structures, we expected hybrid models to provide the most accurate and reliable predictions of extinction risk for both habitat generalists and habitat specialists.

Methods

Species-level data

We used the International Union for Conservation of Nature (IUCN) Red List (IUCN 2021) to classify species as threatened or non-threatened. Threatened species included species categorized as 'Vulnerable,' 'Endangered' or 'Critically Endangered,' whereas non-threatened species included those categorized as 'Least Concern' or 'Near Threatened.' Species categorized as 'Data Deficient,' 'Extinct in the wild,' and 'Extinct' on the Red List were excluded from our analyses. Additionally, we classified species as 'habitat generalist' or 'habitat specialist' based on the information available from the Level 1 IUCN Red List habitat classification scheme (IUCN 2021). Habitat generalists included species that used more than one habitat type as suitable habitat, whereas habitat specialists included all species that used only one habitat type as suitable habitat. Consistent with previous extinction risk analyses (Purvis et al. 2000, Cardillo et al. 2008), we used species' geographic ranges from the IUCN Red List (IUCN 2021) and selected range polygons where the presence of each species was classified as 'Extant' or 'Probably Extant'. Our final dataset retained 4,774 out of 5,787 extant terrestrial mammals, representing 82.5% of all species in the group (IUCN 2021).

Human footprint

We used the recent release of the global human footprint (HFP) maps for the years 2000 and 2013 (Williams et al. 2020) to represent the extent and trends in habitat intactness for each species, using a patch-matrix (Fig. 3.1b), continuum (Fig. 3.1c), and hybrid (Fig. 3.1d) model. The HFP maps provide a 1-km spatial resolution measure of cumulative human pressure ranging from 0 to 50 based on eight pressure layers (Venter et al. 2016): (i) built environments; (ii) intensive agriculture; (iii) pastureland; (iv) human population density; (v) night-time lights; (vi) roads; (vii) railways; and (viii) navigable waterways. Areas free of any human influence (e.g., terrestrial remaining wilderness) are represented by an HFP value of 0, those with low human pressure (e.g., pasture lands) by HFP values of 4 or below, and those with very high-pressure levels (e.g., densely populated semi-urban and urban environments) by HFP values above 20.

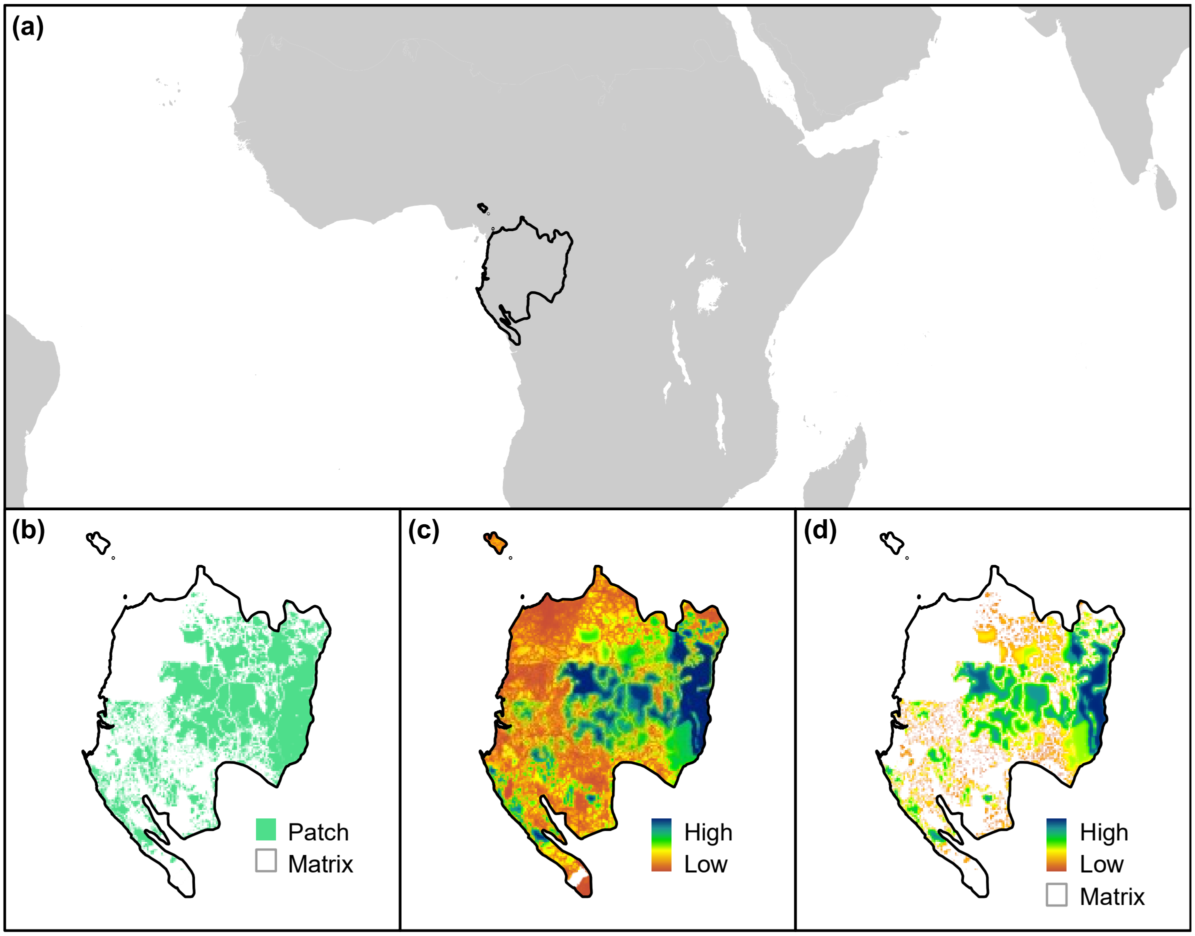

Figure 3.1: An example of habitat intactness models used to predict species extinction risk. (a) This example is based on the geographic range size (polygon delimited in black) of the western gorilla (*Gorilla gorilla*). (b) The patch-matrix model illustrates discrete patches of intact habitat surrounded by an 'inhospitable' matrix. (c) The continuum model depicts a gradient of habitat intactness, ranging from intact habitats (in blue) to degraded habitats (in red). (d) The hybrid model combines characteristics of patch-matrix and continuum models, representing discrete habitat patches and a gradient of habitat intactness within these patches, which is influenced by the matrix condition.

Patch-matrix model as a predictor of extinction risk

We represented habitat intactness as patch-matrix models (Fig. 3.1b) by quantifying the proportion of each species' range overlapping with HFP levels lower than 3. This threshold was used under the assumption that HFP values < 3 corresponded to intact habitat patches and HFP values ≥ 3 to areas of unsuitable or matrix habitat. We used this HFP threshold because the extent of low human footprint levels (i.e., HFP values < 3 out of 50) within a species' range is among the strongest predictors of extinction risk in terrestrial mammals (Di Marco et al. 2018b). Furthermore, this HFP threshold is strongly associated with the greatest declines in mammalian movements (Tucker et al. 2018) and has been used to define intact areas in previous work (Watson et al. 2016, Jones et al. 2018, Beyer et al. 2020, Mokany et al. 2020, Ward et al. 2020, Williams et al. 2020, O'Bryan et al. 2021). Additionally, we quantified the decrease in the proportional overlap between each species' range and low HFP levels from 2000 to 2013 to account for the reduction in habitat intactness. We discarded areas where the extent of low HFP values was lower in 2000 than in 2013, assuming no change in these areas. We only accounted for increases in HFP values as decreases in pressure levels are likely to take time before having a measurable effect on species conservation status, particularly for species with long generation times (Di Marco et al. 2018b).

Continuum model as a predictor of extinction risk

We represented habitat intactness as a continuum model (Fig. 3.1c) for each species using the metric of habitat intactness proposed by Beyer et al. (2020). This metric integrates habitat area, habitat quality, and habitat fragmentation into a single continuous variable, all of which influence the ability of a given habitat to support biodiversity (Ovaskainen and Hanski 2003, Fischer and Lindenmayer 2007, Saura and Rubio 2010, Hanski et al. 2013, Betts et al. 2017). This metric provides information about the contribution of each cell to the overall intactness of a spatial feature (e.g., a species' geographic range) based on an exponential function ($w_i = exp(-\gamma HFP_i)$) that transforms the HFP to quality (Appendix B, Supplementary methods B.1). The habitat intactness metric ranges from 0 to 1, where higher values indicate intact habitats and lower values indicate increasing levels of habitat degradation. The contribution of each cell to intactness (Q'_i) is given by:

$$Q'_i = \frac{\sum_{j \in M_i} (w_i w_j)^z exp(-\beta d_{ij})}{\sum_{j \in M_i} exp(-\beta d_{ij})} \tag{1}$$

where d_{ij} is the distance between cell i and j (in km), M_i is the set of cells falling with a radius of cell i that corresponds to the 99.5% quantile of the exponential distribution (here, 26.5 km), z is an exponent that scales the product to two quantiles, w is a measure of the quality of the cell in the range 0–1, and β is a parameter that determines how the combined value of pairs of cells diminishes as a function of the distance between them. Following Beyer et al. (2020), we used a value of $z = 0.5$ to ensure that the combined weight $(w_i w_j)^z$ was directly proportional to the weight w_i when $i = j$ (i.e., $w_i = (w_i w_j)^z$), and a value of $\beta = 0.2$, which corresponded to a 50% penalty at a separation of 5 km and a 95% reduction of 15 km.

We measured the percentile distribution (i.e., 5th, 10th, 50th, 90th, and 95th percentiles) of values from the habitat intactness metric within each species' range to represent habitat intactness as continuum models. We selected the most explanatory percentile of habitat intactness for both habitat generalists and habitat specialists to compare the continuum model with the patch-matrix and hybrid models in predicting extinction risk (see Statistical analysis;

Appendix B, Fig. B.1). Additionally, we measured the change in the selected percentiles of habitat intactness between 2000 and 2013. As with the patch-matrix model, we discarded areas where habitat intactness values were lower in 2000 than in 2013, assuming no change in these areas.

Hybrid model as a predictor of extinction risk

We represented species' habitat intactness as hybrid models by calculating the percentile distribution of values from the habitat intactness metric within relatively intact habitat patches (i.e., HFP values < 3) across each species' range (Fig. 3.1d). We selected the most explanatory percentile for both habitat generalists and specialists to compare the hybrid model's performance with the patch-matrix and continuum habitat models in predicting extinction risk (see Statistical Analysis; Appendix B, Fig. B.1). Additionally, we measured the change in the selected percentiles of the hybrid model between 2000 and 2013. As with the continuum model, we discarded areas where habitat intactness values were lower in 2000 than in 2013, assuming no change in these areas.

The patch-matrix, continuum, and hybrid models of habitat intactness were obtained through geospatial analyses conducted in Python, using the ArcPy processing module from ArcGIS Pro (ESRI 2022).

Statistical analysis

We used mixed-effects logistic regression to model extinction risk (threatened or not threatened species) as a function of habitat intactness derived from the patch-matrix, continuum, and hybrid models. Measures of habitat intactness were highly correlated ($r > |0.7|$; Appendix B,

Fig. B.2); thus, each regression model tested one model of habitat intactness while controlling for the effects of other variables (Table 3.1) known to influence extinction risk (Cardillo et al. 2005, 2008, Di Marco et al. 2014b, Arregoitia 2016). Consistent with other extinction risk analyses (Betts et al. 2017, Pillay et al. 2022), we fit separate regression models to assess differences in habitat specialization (i.e., habitat generalists versus habitat specialists). Following previous work (Betts et al. 2017, Ripple et al. 2017, Lucas et al. 2019), we included taxonomic orders as random effects to broadly control for phylogenetic non-independence of the observations. All extinction risk models were fit using the generalized linear mixed-effects model (glmer) function from the lme4 package in R (Bates et al. 2015, R Core Team 2023). These models included the same number of predictors (see Table 3.1) to ensure a consistent basis for comparison.

Table 3.1: Description of variables used to predict species extinction risk. We selected the most explanatory percentile from our continuum and hybrid models of habitat intactness to compare how patch-matrix, continuum, and hybrid models predict species extinction risk. (see Appendix B, Fig. B.1).

Variable	Description	Source
Patch-matrix model	Proportion of a species' range overlapping with areas of low human footprint (HFP < 3) in 2000.	Di Marco et al. 2018, Williams et al. 2020
Reduction in the patch-matrix model	Reduction in the proportional overlap between a species' range and areas with low human footprint (HFP < 3) from 2000 to 2013.	Di Marco et al. 2018, Williams et al. 2020

Continuum model	Percentile distribution (5th, 10th, 50th, 90th, and 95th percentiles) of habitat intactness values within a species' range in 2000.	Beyer et al. 2020, Williams et al. 2020
Reduction in the continuum model	Reduction in the percentile distribution (5th, 10th, 50th, 90th, and 95th percentiles) of habitat intactness values within a species' range between 2000 and 2013.	Beyer et al. 2020, Williams et al. 2020
Hybrid model	Percentile distribution (5th, 10th, 50th, 90th, and 95th percentiles) of habitat intactness values within relatively intact habitat patches (HFP < 3) across a species' range in 2000.	Beyer et al. 2020, Williams et al. 2020
Reduction in the hybrid model	Reduction in the percentile distribution (i.e., 5th, 10th, 50th, 90th, and 95th percentiles) of habitat intactness values within relatively intact habitat patches (HFP < 3) across a species' range from 2000 to 2013.	Beyer et al. 2020, Williams et al. 2020
Order	A species' taxonomic order.	IUCN 2021
Range size	Area in square kilometers of a species' distribution.	IUCN 2021
Gestation length	A proxy for a species' reproductive output.	Soria et al. 2021
Weaning age	A proxy for a species' reproductive onset.	Soria et al. 2021

Assessing model performance

We used the area under the receiver operating characteristic curve (AUC) metric to assess the predictive performance of our extinction risk models. This metric reflects true positive rates as a function of false positive rates for a binary classifier (Swets 1988, 2014). We used a spatially blocked cross-validation scheme to calculate AUC values for models of extinction risk for both habitat generalists and habitat specialists. We used this method because it accounts for entire regions as hold-out datasets, reducing the positive effects of dependency on model performance metrics (Bahn and McGill 2013, Cazalis et al. 2022). Additionally, we utilized a ten-fold cross-validation scheme for comparison. For the spatial blocking approach, the probability of a species being threatened was predicted for each of six biogeographic realms (Afrotropic, Australasia, Indomalayan, Nearctic, Neotropic, and Palearctic), with the model fit from all other realms. We only retained those species with the majority (>50%) of their distributions within a realm based on the biogeographic classification of the world proposed by (Dinerstein et al. 2017). We pooled species from the Oceania realm into the Australasia realm because the Oceania realm contained only eight species in our dataset. Following Swets (1988), we considered models with AUC values of 0.5–0.7 as being ‘low accuracy,’ those ranging between 0.7 and 0.9 as ‘useful applications’, and those with values greater than 0.9 as being ‘high accuracy.’

Sensitivity analysis

Species designated as threatened due to small geographic range (i.e., those assessed solely under IUCN Red List Criterion B) can introduce circularity in extinction risk analyses (Cardillo et al. 2005). Thus, we conducted a sensitivity analysis in which we excluded only species classified as threatened under Criterion B alone. This resulted in the exclusion of 242 habitat generalists and 281 habitat specialists. We then compared results from this reduced dataset to those obtained using the full dataset, which included 744 habitat generalists and 486 habitat specialists classified as threatened, and 2,667 habitat generalists and 877 habitat specialists classified as non-threatened.

Results

Overall, our extinction risk models performed well for both habitat generalists and habitat specialists (Appendix B, Fig. B.3). Under a spatially blocked cross-validation scheme, models that included hybrid representations of habitat intactness—along with their temporal decline—demonstrated the highest predictive performance, with an average AUC of 0.83 (95% CI: 0.78–0.88) for habitat generalists and 0.82 (95% CI: 0.75–0.89) for habitat specialists. Ten-fold cross-validation yielded similar results, with hybrid-based extinction risk models achieving an average AUC of 0.85 (95% CI: 0.82–0.87) for habitat generalists and 0.83 (95% CI: 0.81–0.86) for habitat specialists.

Our results were not substantially altered after excluding threatened species assessed solely under Criterion B (Figs. B4, B5), indicating the robustness of extinction risk models to this sensitivity analysis. However, for habitat generalists, models using patch-matrix and continuum representations of habitat intactness, as well as their temporal decline, showed increased AUC values with non-overlapping confidence intervals. This suggests that the exclusion of threatened species assessed solely under Criterion B may partially influence model performance when habitat condition is represented using patch-matrix or continuum approaches.

In contrast, extinction risk models based on hybrid representations remained consistent across all analyses, highlighting their value for extinction risk assessments.

We found a statistically significant negative association between the risk of extinction and the patch-matrix, continuum, and hybrid models of habitat intactness for both habitat generalists (Fig. 3.2a) and habitat specialists (Fig. 3.2b). This association was stronger when habitat intactness was represented by hybrid models, followed by continuum models. Additionally, we found that, regardless of the habitat model, the effect of intactness on the risk of extinction was stronger for habitat specialists. These results remained consistent when we excluded threatened species that met IUCN Red List criterion B alone (Appendix B, Fig. B.6), demonstrating that a simple circular relationship between predictor and response variable did not influence our findings.

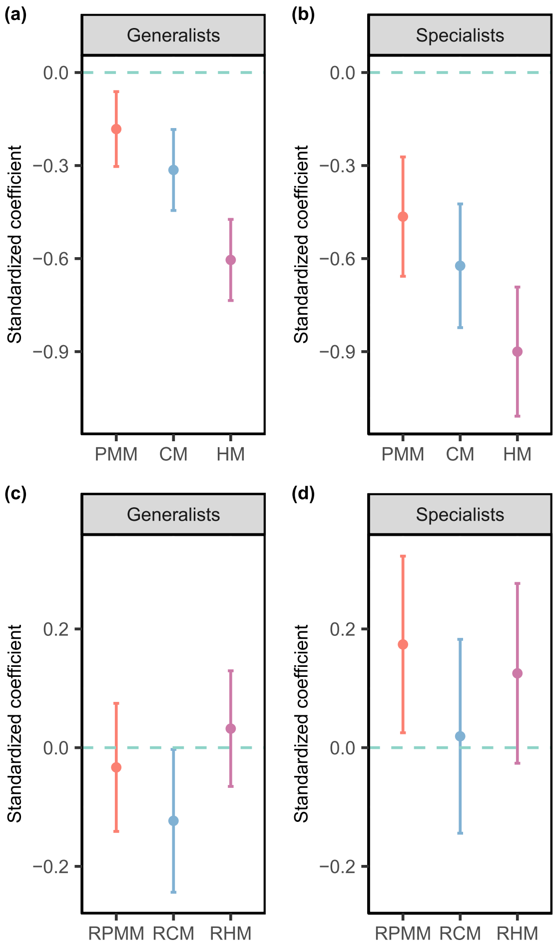

Figure 3.2: Effects of three habitat intactness models (a, b) and their temporal reduction (c, d) on extinction risk for terrestrial mammals classified as habitat generalists and habitat specialists. Each variable is colour-coded according to the habitat model (patch-matrix, continuum, or hybrid model) it represents. Effect sizes were estimated while holding other variables known to influence extinction risk (see Table 3.1) at their mean. All variables were standardized (*z*-transformed) before analysis to ensure comparable results. Error bars represent 95% confidence intervals. The statistical significance of the coefficients is indicated by the absence of overlap between their confidence intervals and zero (dashed green line). Acronyms: patch-matrix model (PMM), continuum model (CM), hybrid model (HM), reduction in the

patch-matrix model (RPMM), reduction in the continuum model (RCM), and reduction in the hybrid model (RHM).

Our results reveal a statistically significant association between extinction risk and the reduction in habitat intactness over time, exclusively when using continuum models for habitat generalists (Fig. 3.2c) and patch-matrix models for habitat specialists (Fig. 3.2d). This association lost significance for habitat generalists but remained statistically significant for habitat specialists after excluding threatened species meeting IUCN Red List criterion B alone (Appendix B, Fig. B.6). These findings support our initial expectations, indicating that habitat specialists are particularly at risk when the size of intact habitat patches decreases over time.

Notably, our results show that the decline in the predicted probability of being threatened was steepest under hybrid models (Fig. 3.3a,b). This suggests that hybrid models of habitat intactness more accurately reflect how small reductions in intactness can lead to rapid increases in extinction risk. This result was consistent for both habitat generalists (Fig. 3.3a) and specialists (Fig. 3.3b), although specialists showed a comparatively greater probability of being threatened when their ranges contained patches with the lowest intactness.

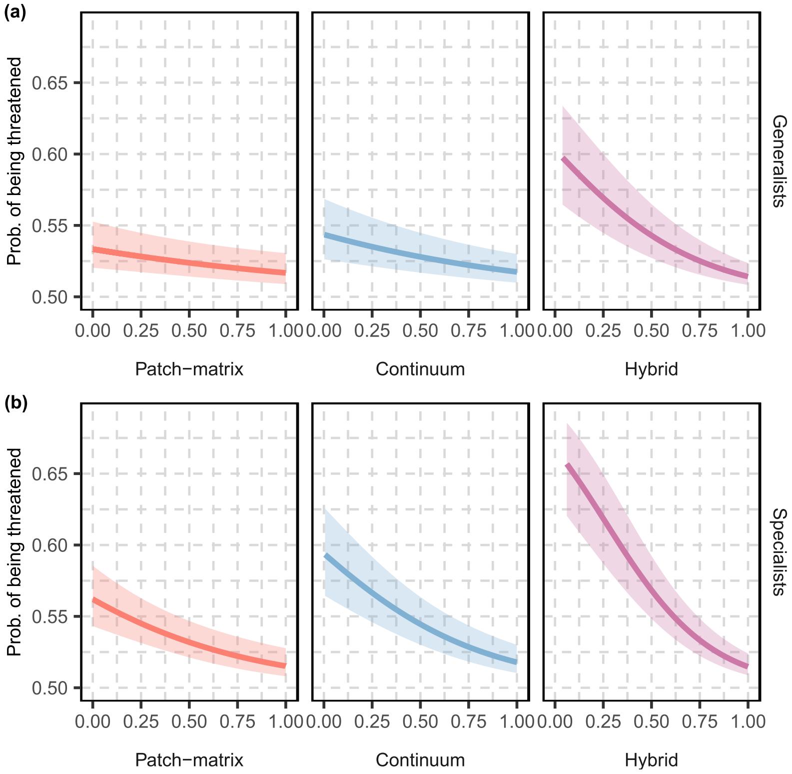

Figure 3.3: Predicted probabilities of a species being threatened as a function of three habitat intactness models for both habitat generalists (a) and habitat specialists (b). Predicted probabilities were estimated while holding other variables known to influence extinction risk (see Table 3.1) at their mean. Variables representing patch-matrix, continuum, and hybrid models were back-scaled to improve results interpretability. Shaded portions represent 95% confidence intervals.

Discussion

Habitat models are fundamental for understanding the impact of human activities on biodiversity, and for informing conservation policies and management strategies (Fischer and Lindenmayer 2006, Brudvig et al. 2017). We found that, regardless of a species' habitat specialization, hybrid models most accurately predicted extinction risk for terrestrial mammals when comparing patch-matrix, continuum, and hybrid representations of habitat intactness on a global scale. These results underscore the untapped potential of conceptual habitat models—particularly hybrid approaches—for improving extinction risk assessments at broad spatial scales. Our findings are consistent with a previous study showing broad support for hybrid approaches (Brudvig et al. 2017), which reinforces the suitability of hybrid models for conceptualizing and interpreting the effects of habitat intactness on biodiversity.

Although these frameworks have often been described as conceptual landscape models (e.g., Price et al. 2009, Brudvig et al. 2017), we apply them in a species-specific context and refer to them as models of habitat intactness. This distinction reflects our focus on quantifying the condition of habitat within each species' range, rather than characterizing landscape structure more broadly. Our interpretation aligns with Fischer and Lindenmayer (2006, 2007), who conceptualized these models as tools to understand how species use habitat across modified environments. Given that species differ widely in their sensitivity to habitat degradation (Henle et al. 2004, Ewers and Didham 2006), understanding how different representations of intactness influence extinction risk is critical for anticipating biodiversity loss.

Contrary to our expectations, we found that continuum models were better than patch-matrix models at predicting extinction risk for habitat specialists. One plausible explanation for this finding is that some human-modified areas can provide suitable habitats and act as a buffer mechanism against extinction not only for habitat generalists but also for habitat specialists, particularly when these areas exhibit structural similarities to their preferred habitat. This notion is supported by previous studies demonstrating the conservation potential of well-managed production landscapes, where many habitat specialists can persist (e.g., Daily et al. 2001, 2003, Benton et al. 2003, Hole et al. 2005).

In our study, using the HFP and its associated metrics of habitat intactness provided a unique opportunity to test the relationship between conceptual habitat models and extinction risk. However, the exclusion of variables associated with pressure not captured by the HFP—such as biological invasions, overexploitation, and climate change—could have limited the predictive success of our models. Considering the inherent challenge of accurately mapping these influential variables (Belote et al. 2020), we acknowledge this limitation.

Our results suggest that the choice of habitat model can influence the empirical relationship between habitat intactness and extinction risk. For example, we found that the probability of a species being threatened was notably greater under conditions of lower habitat intactness when represented by the hybrid model rather than the patch-matrix model, regardless of a species' habitat specialization. This finding suggests that conservation priorities should be focused not only on minimizing human disturbances within relatively intact habitat patches but also on enhancing the structural similarity between intact habitat and the surrounding matrix. This approach to managing the matrix habitats aligns with a recent study showing that high-value biodiversity habitats in both intact and highly modified regions require focused conservation commitments and actions to halt ongoing extinctions (Mokany et al. 2020).

Our results indicate that habitat specialists were especially vulnerable to the reduction in intactness when modeled using the patch-matrix approach, even after excluding threatened species assessed solely under criterion B. This suggests that including the temporal reduction of habitat intactness as a patch-matrix model has the potential to enhance model performance when predicting extinction risk, particularly for habitat specialists.

Our findings reveal a statistically significant negative relationship between habitat intactness and extinction risk across our patch-matrix, continuum, and hybrid models, with non-threatened species likely to become threatened if current rates of the HFP persist into the future (Williams et al. 2020, Mu et al. 2022). These results point toward the possibility of future work to use our habitat models to predict extinction risk under alternative global scenarios of socioeconomic growth (Watson and Venter 2019). However, undertaking such an endeavor would require generating future projections of the HFP and predicting shifts in species distribution in response to climate and land-use changes (Visconti et al. 2016, Beyer and Manica 2020).

Regardless of a species' habitat specialization, we found that terrestrial mammals are more likely to be threatened if their ranges contain habitat patches with decreasing structural intactness. These results may be attributed to the combined impact of habitat loss and degradation, which indirectly give rise to additional threats such as hunting, disease spread, selective logging, wildfires, and invasive species (Barlow et al. 2016, Betts et al. 2017). This indicates that the ability of intact habitat patches to support biodiversity gradually decreases with the increasing intensity of human pressure around them, highlighting that in addition to efforts to minimize human disturbance, there is a need for targeted management strategies in the surrounding matrix.

Chapter 4: Mapping the conservation potential of the matrix for terrestrial mammals

Abstract

Conservation strategies have long prioritized primary habitats, often overlooking the matrix—the surrounding areas of lower habitat suitability—where many species may still persist. This oversight can compromise species persistence and ecological connectivity, potentially undermining long-term biodiversity conservation. Here, we present the first global assessment of species richness within the matrix for terrestrial mammals. Using high-resolution habitat maps for 5,439 species, we identify species-rich matrix areas, where species richness is greater than in suitable habitats, and delineate matrix-based richness hotspots—defined as the top 5% of grid cells with the highest richness values within these areas—for all mammals, declining mammals, and threatened mammals. We found that species-rich matrix areas cover 12% of Earth's terrestrial surface, yet matrix hotspots occupy just 1%. Importantly, over half of terrestrial mammals potentially occur in these matrix hotspots. Notably, hotspots defined solely by threatened mammals contain nearly as many species as all hotspot types combined. Matrix areas identified as having high conservation potential—based on overlapping richness hotspots—are primarily concentrated in tropical strongholds such as the Amazon Basin, Colombian Tropical Andes, Brazilian Atlantic Forest, and Albertine Rift. Nearly half of these areas face intense human pressure and remain outside protected or conserved area networks, suggesting they represent important opportunities for biodiversity conservation. Our results highlight the critical importance of integrating the matrix into global biodiversity conservation strategies.

Introduction

Industrial-scale human activities have transformed between 75% and 95% of Earth's ice-free land surface (Venter et al. 2016, Ellis et al. 2021, Ellis 2021), leading to increasingly fragmented landscapes where natural ecosystems are embedded within human-modified environments (Perfecto and Vandermeer 2008). As a result, many species are now confined to—or must frequently move through—landscapes dominated by agriculture, urbanization, and other forms of human land use (Tucker et al. 2018, Kremen and Merenlender 2018, Galán-Acedo et al. 2019, Torres-Romero et al. 2020, Britnell et al. 2023, Zhang et al. 2024). These large-scale transformations have been widely recognized as the primary drivers of an accelerating biodiversity crisis (Newbold et al. 2015, Maxwell et al. 2016, Jaureguiberry et al. 2022), with extinction rates estimated to be tens to thousands of times higher than historical background levels (Barnosky et al. 2011, Pimm et al. 2014, De Vos et al. 2015, Ceballos et al. 2015). As habitat loss and fragmentation continue to intensify, the capacity of species to survive beyond primary habitats—natural and semi-natural areas characterized by minimal human disturbance and high ecological integrity—is emerging as a key determinant of biodiversity persistence in the Anthropocene (Gardner et al. 2009, Prevedello and Vieira 2010, Watling et al. 2011).

The areas surrounding primary habitats—often referred to as the matrix—have traditionally been treated as unsuitable or ecologically irrelevant (MacArthur and Wilson 1967, Haila 2002). However, a growing body of research challenges this view, demonstrating that the matrix can either buffer or exacerbate the impacts of habitat loss and fragmentation, depending on their quality, structure, and spatial configuration (Ricketts 2001, Prugh et al. 2008, Prevedello and Vieira 2010, Watling et al. 2011, Driscoll et al. 2013, Ramírez-Delgado et al. 2022). High-contrast matrices, such as intensive agriculture or urban development, can increase isolation and mortality risk (Battin 2004), whereas low-contrast matrices, like agroforestry systems or secondary forests, can facilitate movement, reduce edge effects, and supplement habitat resources (Daily et al. 2003, Perfecto and Vandermeer 2008). Despite this growing recognition, global conservation strategies remain largely focused on primary habitats (Margules and Pressey 2000, Brooks et al. 2006, Gibson et al. 2011, Martin et al. 2012, Watson et al. 2018a, Di Marco et al. 2019), often overlooking the ecological value and conservation potential of the surrounding matrix (Prugh et al. 2008, Franklin and Lindenmayer 2009, Prevedello and Vieira 2010, Kremen and Merenlender 2018, Arroyo-Rodríguez et al. 2020). This narrow focus limits our ability to identify conservation opportunities, particularly in human-modified landscapes where many species now persist (Tucker et al. 2018, Kremen and Merenlender 2018, Galán-Acedo et al. 2019, Torres-Romero et al. 2020, Britnell et al. 2023, Zhang et al. 2024).

Here, we present a global assessment of terrestrial mammal species richness within the matrix, defined as areas within a species' geographic range but outside its suitable habitat. We focused on terrestrial mammals because of the availability of consistent, species-level habitat data (Lumbierres et al. 2022b). Using Area of Habitat (AOH) maps at 100-m spatial resolution for 5,439 species (Lumbierres et al. 2022b) and geographic range maps from the International Union for Conservation of Nature (IUCN 2024), we mapped species richness across suitable habitats and the matrix. AOH maps delineate suitable habitat by combining species-specific ecological requirements, such as elevation range, land-cover type, and known habitat associations (Rondinini et al. 2011, Brooks et al. 2019, Lumbierres et al. 2022b). However, AOH maps assume that species distributions strictly align with areas identified as suitable, potentially overlooking occurrences in suboptimal or transitional habitats, microhabitat variations, or species’ ecological plasticity (Rondinini et al. 2011, Lumbierres et al. 2022b). This limitation may underestimate the actual extent of species' habitat use and their ability to persist in or utilize areas classified as unsuitable or marginal. We therefore identified species-rich matrix areas, defined here as locations with disproportionately greater richness of terrestrial mammals compared to suitable habitats. Based on IUCN Red List assessments (IUCN 2024), we delineated richness hotspots within these species-rich matrix areas for three groups: all mammals, mammals with declining population trends, and mammals with threatened status. By overlapping these hotspots, we classified matrix areas as having high, moderate, or low conservation potential and further assessed them in terms of human pressure (Gassert et al. 2023) and conservation coverage (UNEP-WCMC and IUCN 2023). Through this mapping, we identified matrix areas as critical yet underrecognized components of global conservation strategies, where habitat restoration or requalification efforts could deliver significant benefits to terrestrial mammal conservation.

Methods

Species area of habitat

The extent of suitable habitat and matrix areas for each terrestrial mammal was derived from AOH maps developed by Lumbierres et al. (2022b). These maps, created at a 100-m spatial resolution for the year 2015, delineate suitable habitat areas within each species' geographical range by integrating species-specific habitat preferences and elevational limits from IUCN Red List data, as well as high-resolution land cover data (Lumbierres et al. 2022a, b). Validation against known occurrence points was possible for only a subset of terrestrial mammal species (8% of those mapped), owing to the limited availability of high-accuracy point locality data (Lumbierres et al. 2022b). Within this subset, ~95% of AOH maps performed better than random within species' ranges, indicating broad consistency between mapped suitable habitat and observed occurrences. While this performance threshold represents a minimum benchmark rather than a high predictive accuracy metric, the maps provide a consistent and spatially explicit basis for global-scale biodiversity assessments, making them well suited for the aims of this study.

Given that AOH maps only capture suitable habitat for each species, the extent of the matrix was defined using species range maps from the IUCN Red List (IUCN 2024). Following established criteria (IUCN 2020, Lumbierres et al. 2022b), we selected polygons classified as 'Extant' or 'Probably Extant' and labeled as 'resident,' 'Reintroduced (resident),' or 'Assisted Colonisation (resident)'. Pixels outside suitable habitat (as defined by AOH maps) but within the selected range polygons were classified as unsuitable or matrix areas.

To ensure consistency between the AOH maps and the range data, we excluded 41 AOH maps from the initial dataset of 5,481. These exclusions resulted from taxonomic updates, spatial mismatches between AOH maps and range maps, changes in species range classifications, and cases where AOH maps lacked corresponding range data. As a result, our final dataset included 5,439 species, representing about 94% of the world's extant terrestrial mammals (IUCN 2024).

From this final dataset, we then delineated suitable habitat and matrix areas within each species' range. To minimize the influence of potential inconsistencies in the AOH data, small contiguous groups of pixels (<4 adjacent pixels of the same class) that may have resulted from inconsistencies in the underlying datasets of the AOH maps were removed. These small groups were replaced with the value of the largest and nearest contiguous group, determined using the eight-neighbor rule. In line with previous work (Crooks et al. 2011, 2017, Ramírez-Delgado et al. 2022), this process minimized the influence of isolated pixel groups and enhanced the computational efficiency of our analyses.

Species richness maps

We generated species richness maps for matrix areas by aggregating pixels classified as 'unsuitable' for each species of terrestrial mammal. Richness maps were created for three groups: all mammals (Appendix C, Fig. C.1a), mammals with declining population trends (Appendix C, Fig. C.1b), and mammals with threatened status (Appendix C, Fig. C.1c). Conservation status and population trend data were sourced from the IUCN Red List (IUCN 2024). Species listed as 'Vulnerable,' 'Endangered,' or 'Critically Endangered' were categorized as threatened, while those with a population trend labeled 'Decreasing' were categorized as declining.

In addition to the matrix richness maps, we generated a suitable habitat richness map for the all-mammal group (Appendix C, Fig. C.4). This map served as a broad reference for identifying species-rich matrix areas, as detailed in the following section.

Species-rich matrix areas

Using the all-mammal group, we calculated pixel-level species richness separately for matrix areas (Appendix C, Fig. C.1a) and suitable habitats (Appendix C, Fig. C.2), generating two global richness maps. For each pixel, we computed a richness ratio by dividing the matrix richness value by the suitable habitat richness value at the same spatial location. Pixels with richness ratios greater than 1, indicating greater richness in the matrix relative to suitable habitats, were classified as species-rich matrix areas. These areas represented locations in the matrix with disproportionately greater species richness compared to suitable habitats. We then extracted species richness values within these species-rich matrix areas from matrix-based richness maps for each species group (i.e., all mammals, mammals with declining population trends, and mammals with threatened status).

Hotspots of species richness

Following previous studies (e.g., Orme et al. 2005, Ceballos and Ehrlich 2006, Jenkins et al. 2013), we identified hotspots of species richness within species-rich matrix areas by selecting the top 5% of pixels with the highest richness values for each species group. Pixels were classified as hotspots only if they formed contiguous clusters with a minimum area of 10 km^2, a conservative threshold broadly aligned with generalized minimum-area guidelines suggested to support mammal assemblages in global biodiversity assessments (Verboom et al. 2014). We used an iterative threshold optimization process to systematically refine the richness threshold, ensuring that the final hotspot coverage closely approximated 5% for each species group while meeting clustering requirements. To test the sensitivity of our results, we also evaluated alternative thresholds using the top 2.5% and top 10% of pixels.

Levels of conservation potential within matrix areas

Levels of conservation potential within matrix areas were identified based on spatial overlap among hotspot types. Areas with high conservation potential corresponded to locations where all three hotspot types (all mammals, mammals with declining population trends, and mammals with threatened status) overlapped, areas with moderate conservation potential where any two overlap, and areas with low conservation potential where only a single hotspot type was present with no overlap.

Species-level hotspot representation

To assess species representation across hotspot types, we identified species whose matrix area spatially overlapped with any of the three hotspot types. We considered a species to occur in a hotspot if its matrix (defined as areas within the species' range but outside its suitable habitat) intersected or overlapped hotspot boundaries. For each species, we determined whether its matrix area intersected one, two, or all three hotspot types, based on spatial overlays. Each species was assigned to a single overlap category corresponding to the unique combination of hotspot types its matrix intersected. These species-level assignments were then used to quantify representation across individual hotspot types and their combinations.

Human pressure in matrix hotspots

We used the human footprint (HFP) dataset (Gassert et al. 2023) to quantify the influence of human pressures within matrix areas identified as having conservation potential. Built on previous HFP mapping efforts (Venter et al. 2016, Williams et al. 2020), this dataset provides a standardized measure of human pressure on terrestrial environments by integrating data on eight anthropogenic pressures: (i) built environments, (ii) cropland, (iii) pastureland, (iv) human population density, (v) night-time lights, (vi) roads, (vii) railways, and (viii) navigable waterways. Developed at a 100-m spatial resolution for the years 2015–2019 and 2020, the maps in this dataset assign HFP scores ranging from 0 (minimal human influence) to 50 (maximum human influence).

For our analysis, we used the 2015 HFP map to ensure temporal consistency with the AOH maps. Following previous studies (Di Marco et al. 2018b, Mokany et al. 2020, Ramírez-Delgado et al. 2022, Gassert et al. 2023), HFP scores from this map were classified into three categories to represent varying levels of human impact: intact (HFP ≤ 1), low disturbance (1 < HFP < 3), and highly modified (HFP ≥ 3). We specifically applied a threshold of HFP ≥ 3 to identify highly modified areas, as this threshold has been shown to be the strongest predictor of extinction risk transitions in terrestrial mammals (Di Marco et al. 2018b). To quantify human influence within matrix areas with conservation potential, the HFP categories were spatially overlaid on these zones.

Conservation coverage of matrix hotspots

We used spatial data from the World Database on Protected Areas (WDPA) and the World Database on Other Effective area-based Conservation Measures (WD-OECM) (UNEP-WCMC and IUCN 2023) to assess conservation coverage within matrix hotspots.

Following established guidelines (Butchart et al. 2015, Runge et al. 2015, Protected Planet 2025), we excluded protected areas (PAs) and other effective area-based conservation measures (OECMs) entries that did not meet international definitions of PAs or OECMs. Specifically, we removed sites with unknown status, proposed designations, marine-only sites, the marine portions of coastal sites, and sites lacking defined boundaries. Sites represented only by point data were converted into circular polygons based on reported area size. Each dataset (PAs and OECMs) was processed independently and then combined to create a third, integrated layer representing all conserved areas (PAs + OECMs).

All three datasets were rasterized at 100-m spatial resolution to match the resolution of the AOH and HFP datasets. We then generated binary raster layers classifying land as either protected, OECM-designated, or conserved (PAs + OECMs), and overlaid these layers with the matrix conservation potential map stratified by human footprint category (intact, low-disturbance, and highly modified). For each level of conservation potential—defined by spatial overlap among hotspot types, where high corresponds to overlap of all three types, moderate to overlap of any two types, and low to only one—we calculated the proportion of area under protection, OECM designation, or both combined, overall and within each footprint category.

All spatial data were initially processed in the WGS 1984 coordinate system and reprojected to the Mollweide equal-area projection for consistent area calculations. Geospatial analyses were performed using ArcPy (ESRI 2024) and the *wdpar* package in R (Hanson 2022, R Core Team 2023).

Results

Global patterns of terrestrial mammal concentration in the matrix

We found that species-rich matrix areas covered approximately 12% of the global terrestrial area (excluding Antarctica) and were predominantly located in tropical and subtropical regions (Fig. 4.1a–c). This pattern was evident across all mammals (Fig. 4.1a), mammals with declining population trends (Fig. 4.1b), and those with threatened status (Fig. 4.1c), with the highest concentrations occurring in parts of Central and South America, West and Central Africa, and Southeast Asia.

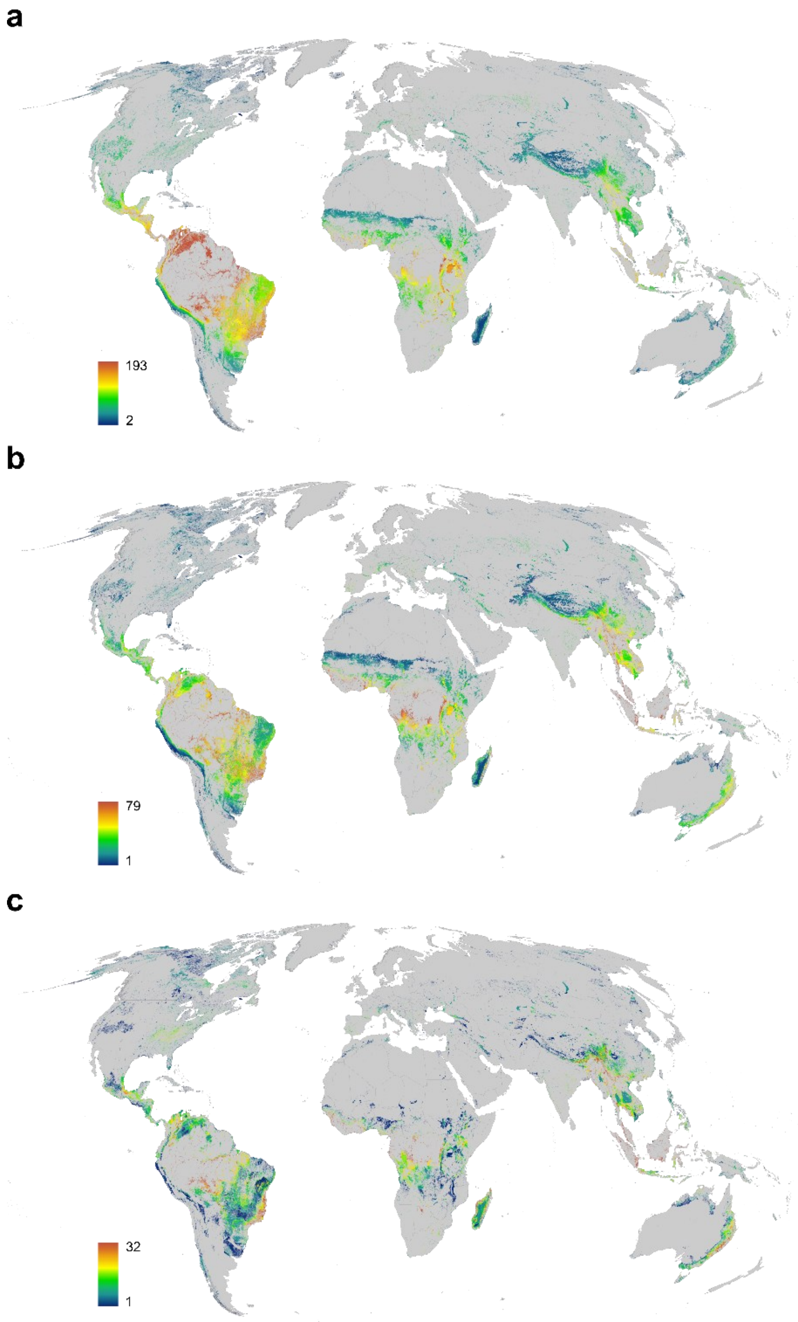

Figure 4.1: Global distribution of species richness within species-rich matrix areas for terrestrial mammals. Species richness is shown for all species (a), species with declining population trends (b), and species with threatened status (c).

Hotspots of species richness, defined as the top 5% of grid cells with the highest richness values within species-rich matrix areas, revealed even more pronounced patterns of species concentration (Fig. 4.2a–c). For all mammals, hotspots were primarily located in tropical regions of South America and Africa, with particularly high concentrations in the Tropical Andes, the Colombian Caribbean, and the Llanos (Fig. 4.2a). In contrast, hotspots for mammals with declining population trends were more scattered and broadly distributed across South America, sub-Saharan Africa, and Southeast Asia, extending into the Eastern Himalayas and Indo-Burma (Fig. 4.2b). Hotspots for threatened mammals overlapped in part with those for mammals with declining population trends and showed a wider distribution across tropical and subtropical regions, including parts of Central America, Madagascar, and eastern Australia (Fig. 4.2c).

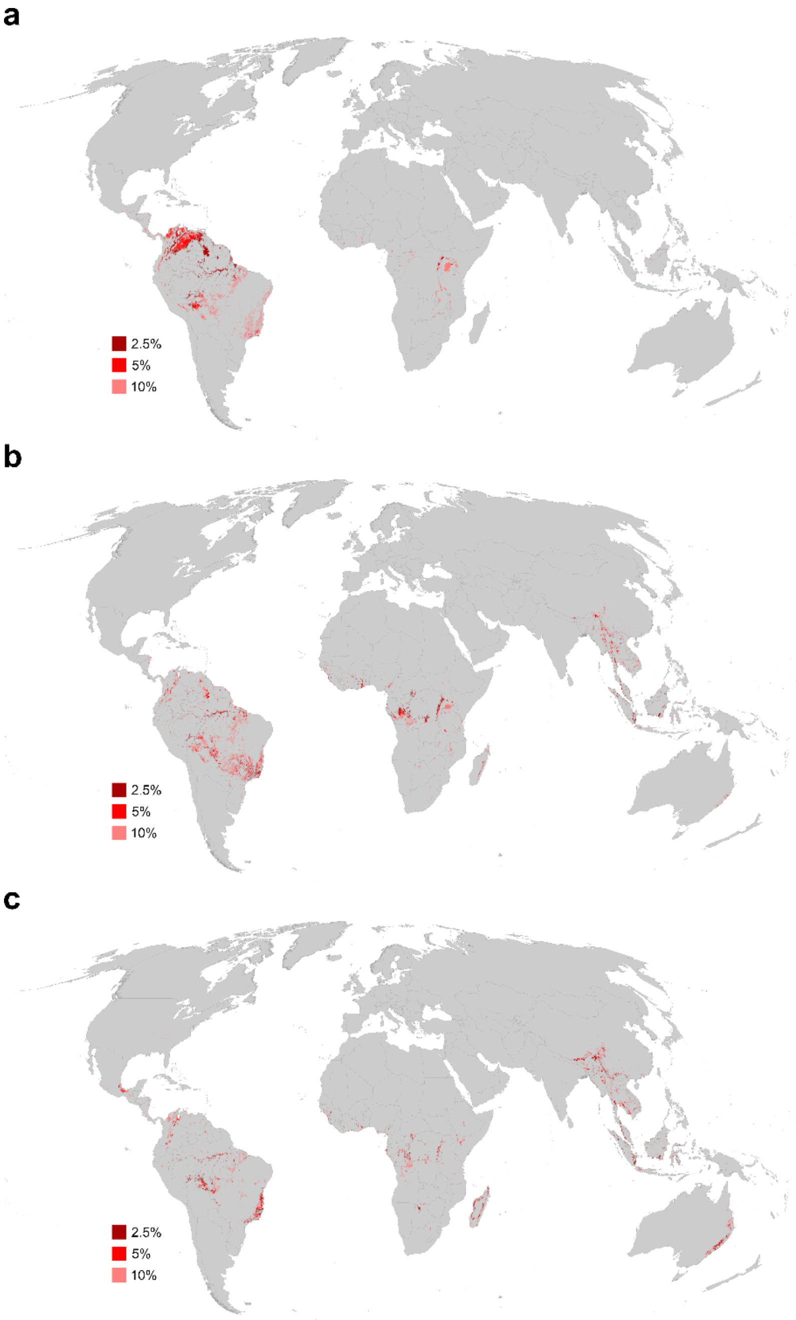

Figure 4.2: Hotspots of species richness within species-rich matrix areas for terrestrial mammals. Hotspots are shown for all mammals (a), mammals with declining population trends (b), and mammals with threatened status (c). Dark red represents the top 2.5% of grid cells with the highest richness values for each species group, red (including dark red) represents the top

5%, and pink (including both red and dark red) represents the top 10%. All hotspots were aggregated into contiguous clusters with a minimum area of 10 km².

A total of 3,419 species—approximately 59% of all extant terrestrial mammals—had matrix areas that overlap with at least one of the three hotspot types (Table 4.1). Collectively, the three hotspot types spanned 1.65 million km², representing 10% of the global extent of species-rich matrix areas and just 1% of the Earth's total terrestrial surface (excluding Antarctica). Notably, hotspots based solely on threatened species captured nearly as many species as the combined total across all three hotspot types, differing by only 3%. This pattern held true across alternative hotspot thresholds (Appendix C, Table C.1), suggesting that threatened species hotspots could serve as effective surrogates for broader conservation efforts within species-rich matrix areas.

Table 4.1: Geographic coverage and species representation of hotspot types. The table shows the total area of each hotspot type and the number of species whose matrix area overlapped with each hotspot type. Numbers in parentheses indicate the percentage of each hotspot type relative to the global extent of species-rich matrix areas (15,922,965 km²), or the percentage of overlapping species relative to the total number of extant terrestrial mammals (5,808 species worldwide). Slight differences in area across hotspot types reflect clustering requirements and the threshold optimization process (see Methods).

Hotspot type	Area (km²)	Number of species
All species	799,277 (5.0)	1,918 (33.0)
Declining trend	818,964 (5.1)	2,836 (48.8)

Threatened status	702,029 (4.4)	3,255 (56.0)
Total in all hotspots	1,655,469 (10.4)	3,419 (58.9)

Matrix areas with conservation potential

The spatial overlap among the three hotspot types was low overall (Fig. 4.3a,b). Areas with high conservation potential—where all three hotspot types overlapped—accounted for only 7% of the total hotspot extent. Moderate conservation potential areas, defined by overlap between two hotspot types, accounted for 26%, while low conservation potential areas, identified by only a single hotspot type, accounted for the majority (67.1%).

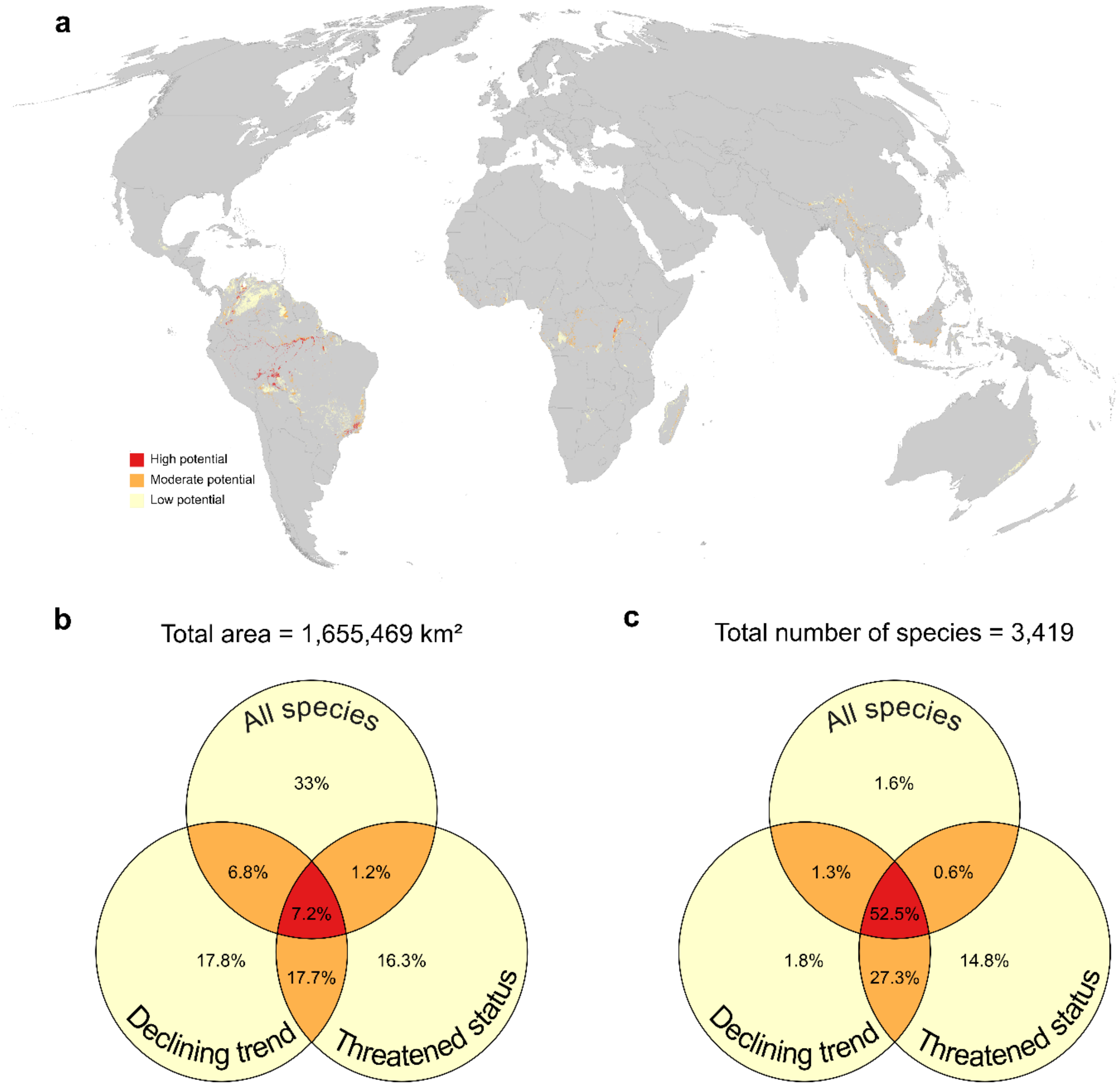

Figure 4.3: Overlap of hotspot types and conservation potential in matrix areas. The map shows the global distribution of species-rich matrix areas, categorized into levels of conservation potential based on spatial overlap among three hotspot types: all mammals, mammals with declining population trends, and mammals with threatened status (a). Venn diagrams show the spatial overlap among hotspot types (b) and the number of species whose matrix habitat overlapped one, two, or all three types (c), respectively. Each species was counted only once, based on the unique combination of hotspot types overlapping its matrix habitat (e.g., one, two,

or all three types), and was assigned to the corresponding category. Areas of high conservation potential corresponded to overlaps among all three hotspot types, moderate conservation potential to overlaps between any two types, and low conservation potential to areas identified by a single hotspot type.

Areas with high conservation potential harboured 53% of all mammals whose matrix habitats overlapped hotspot areas, while areas with moderate and low conservation potential accounted for 29% and 18%, respectively (Fig. 4.3c). Notably, 18% of species with matrix habitat in hotspots occurred exclusively within a single hotspot type, with the majority (14.8%) found only in hotspots for species with threatened status. A total of 932 species occurred in both hotspots for species with declining populations and those for threatened species, suggesting that these categories frequently overlap and that many threatened species are already experiencing ongoing population declines. These patterns were consistent across different hotspot thresholds (Appendix C, Fig. C.3), further highlighting the strong association between population declines and threat status.

Our map of conservation potential in matrix areas showed that areas of high conservation potential were primarily concentrated within a few tropical strongholds, including parts of the Amazon Basin, the Colombian Tropical Andes, the Brazilian Atlantic Forest, and the Albertine Rift (Fig. 4.3a). Areas of moderate conservation potential were more widely distributed but still predominantly located in tropical regions across South America, Central Africa, and Southeast Asia. In contrast, areas of low conservation potential were the most extensive, spanning Central and South America, sub-Saharan Africa, the Eastern Himalayas, Indo-Burma, and eastern Australia.

Human footprint and conservation coverage in matrix areas with conservation potential

When we mapped the conservation potential of matrix areas against human footprint categories (Gassert et al. 2023)—'intact', 'low-disturbance', and 'highly modified'—we found that these areas were predominantly highly modified, although notable subregional variations existed (Fig. 4.4a–d). In parts of Brazil's Amazon (Fig. 4.4a) and Atlantic Forest (Fig. 4.4b), matrix areas with high, moderate, and low conservation potential were widespread and predominantly highly modified. However, scattered remnants of intact and low-disturbance matrix persisted, creating a mosaic of conditions. In the Western Congolian forest–savanna region (Fig. 4.4c), matrix areas with low conservation potential remained largely intact, though interspersed with more disturbed areas. In Sumatra's forests (Fig. 4.4d), matrix areas with moderate conservation potential dominated and were almost entirely highly modified, with only small patches of intact and low-disturbance matrix remaining.

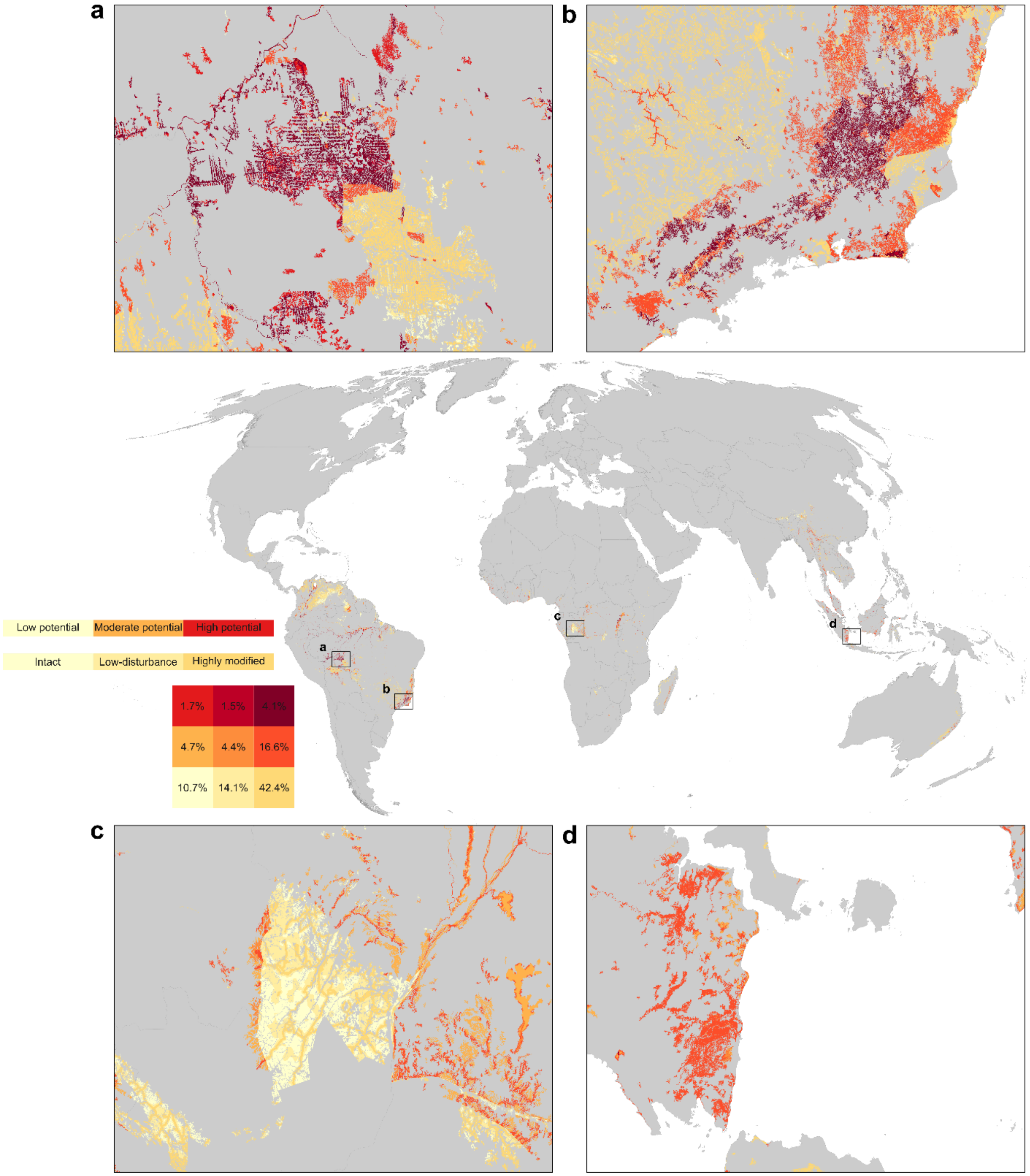

Figure 4.4: Human footprint within matrix areas with conservation potential. The map shows the global distribution of matrix areas with high, moderate, and low conservation potential, categorized by human pressure levels: intact, low-disturbance, and highly modified. Insets show examples from Brazil’s Amazon (a) and Atlantic Forest (b), the Western Congolian

forest-savanna mosaic (c), and Sumatra's forests (d). Human pressure levels were derived from the 2015 global HFP map developed by Gassert et al. (2023) at a 100-m spatial resolution. For details on thresholds used to define each human pressure level, see Methods.

Across all levels of conservation potential, matrix areas remained predominantly unprotected and highly modified (Appendix C, Fig. C.4a). PAs covered only a fraction of matrix areas with high conservation potential, with 49% of this land unprotected and highly modified, and just 7% both protected and intact. Matrix areas with moderate and low conservation potential showed similar patterns, with unprotected, highly modified conditions accounting for 58% and 54%, respectively. OECMs offered only limited additional coverage (Appendix C, Fig. C.4b), and the matrix areas they covered were predominantly highly modified.

Combining PAs and OECMs—hereafter referred to as conserved areas—slightly improved overall conservation coverage but did not substantially alter the broader pattern (Appendix C, Fig. C.4c). Non-conserved and highly modified matrix areas remained the most common condition, accounting for 48% of matrix areas with high conservation potential, 57% with moderate conservation potential, and 52% with low conservation potential. Even where matrix areas were conserved, they were predominantly within highly modified landscapes. Among matrix areas with high conservation potential, 8% were both conserved and highly modified, while only 7% were both conserved and intact. These trends were consistent across other levels of conservation potential, with the majority of conserved matrix areas situated in areas of high human pressure.

Discussion

Our study presents a global framework for identifying conservation opportunities within the matrix, offering new insights into global patterns of the species richness of terrestrial mammals within these areas. We find that species-rich matrix areas cover approximately 12% of Earth’s land surface (excluding Antarctica), yet richness hotspots—largely concentrated in tropical and subtropical regions—cover just around 1%. Importantly, more than half of all terrestrial mammal species may occur within at least one of these hotspot types, with hotspots identified solely by threatened species containing nearly as many species as all hotspot types combined. Matrix areas with high conservation potential, defined by the overlap of all three hotspot types, are limited in extent but potentially support disproportionately high species richness, particularly in regions such as the Amazon Basin, the Colombian Tropical Andes, the Brazilian Atlantic Forest, and the Albertine Rift. However, nearly half of these matrix areas remain highly modified and poorly represented within existing protected or conserved area networks, underscoring the urgent need to explicitly integrate matrix areas into global biodiversity conservation strategies.

While our analysis partially covers regions traditionally recognized as biodiversity hotspots (Myers et al. 2000, Ceballos and Ehrlich 2006, Jenkins et al. 2013), it offers a novel perspective by focusing on species richness within the matrix. Rather than relying solely on species range maps, we used AOH data (Lumbierres et al. 2022b) to differentiate between suitable habitat and matrix areas within species’ ranges, an approach known to provide more refined and ecologically relevant representations than estimates derived from geographic ranges alone, particularly in extensively modified regions (Rondinini et al. 2011). This distinction allowed us to identify conservation opportunities that might otherwise be overlooked if biodiversity value is assumed to be confined solely to suitable habitats. By integrating HFP (Gassert et al. 2023) and conservation coverage data (UNEP-WCMC and IUCN 2023), our analysis offers a more nuanced picture of where biodiversity is not only concentrated but also under pressure and poorly represented within existing formally recognized conservation networks. Together, these elements position our framework as a complement to existing hotspot analyses, extending their value by identifying overlooked components of the landscape that are critical for biodiversity representation and long-term resilience (Brooks et al. 2006, Kremen et al. 2008, Mokany et al. 2020).

Our study advances global conservation assessments by applying a finer spatial grain (100 meters) for AOH maps (Lumbierres et al. 2022b). This resolution represents a substantial increase in spatial detail compared to influential global studies (Myers et al. 2000, Ceballos and Ehrlich 2006, Jenkins et al. 2013), which typically relied on coarser spatial data, often ranging from 10 to 100 km in grain size. We recognize, however, that finer spatial resolution alone does not inherently guarantee greater ecological accuracy or realistic habitat suitability. Indeed, AOH maps are simplified representations of habitat suitability, primarily suited for global biodiversity assessments rather than detailed, species-specific management planning. Nevertheless, the high-resolution analysis presented here provides enhanced localization of global species richness patterns, revealing spatial details likely missed by coarser analyses. While this resolution is particularly valuable for identifying general patterns in fragmented or rapidly changing landscapes—where conservation strategies often depend on spatially explicit information (Rouget 2003, Kremen et al. 2008, Tanhuanpää et al. 2023, Pla et al. 2024, Carruthers-Jones et al. 2025)—we emphasize caution in interpreting these results as directly indicative of fine-scale ecological processes or habitat suitability at local scales.

Empirical validations highlight that, although broadly accurate, AOH maps do not capture all species occurrences. For terrestrial mammals, validation against known occurrence points was possible for only a subset of species (8% of those mapped), owing to the limited availability of high-accuracy point locality data (Lumbierres et al. 2022b). Within this subset, ~95% of maps performed better than random within species' ranges—a minimum performance benchmark rather than a high predictive accuracy metric. Consistent with these limitations, our analyses reveal that matrix areas can contain high mapped species richness, reinforcing their ecological relevance and underscoring the value of incorporating these areas into global conservation planning beyond traditional habitat suitability boundaries.

Our findings challenge the expectation that species richness peaks exclusively in intact habitats, suggesting instead that many highly modified matrix areas can also support relatively high levels of terrestrial mammal richness. This pattern aligns with the well-established 'winners and losers' framework, which highlights how some species benefit from human-driven landscape changes due to increased resource availability, altered predation dynamics, and species filtering (Fisher and Burton 2018, Kremen and Merenlender 2018, Tucker et al. 2021). Moreover, the relationship between human footprint and ecological intactness is not always straightforward (Belote et al. 2020). Many areas with a high human footprint still support high species richness and retain relatively intact mammal assemblages, particularly in highly productive environments or regions with a long history of human-wildlife coexistence (Belote et al. 2020, Torres-Romero et al. 2020, Zhang et al. 2024). For example, in the Peace–Moberly region of northeast British Columbia, Nitschke (2008) found that across an extensively developed landscape, 22% of species experienced declines in modelled habitat while the remainder demonstrated increases, indicating that while some species experienced habitat loss, others were able to persist or even benefit under substantial human modification. Proximity to intact habitats may also play a role, as species can spill over into adjacent matrix areas when habitat boundaries are permeable, enabling temporary use or colonization of suboptimal but accessible habitats (Cook et al. 2002, Brotons et al. 2003, Ewers and Didham 2006). These findings suggest that certain modified habitats, particularly those embedded within heterogeneous or productive landscapes, can play a significant role in sustaining terrestrial mammal biodiversity, challenging conventional assumptions that equate human modification with low ecological value.

Our approach identified hotspots within the matrix based on species richness for all terrestrial mammals in the database, mammals with declining population trends, and mammals with threatened status. We acknowledged that these categories were not mutually exclusive, as declining and threatened mammals constituted subsets of the broader ‘all terrestrial mammals’ group. In practice, a substantial proportion of threatened species are also experiencing population declines, particularly those listed under IUCN Criterion A (population reduction) and, in many cases, Criteria B or C, both of which require evidence of continuing decline. This close alignment in listing criteria contributes to considerable overlap between these groups. Nevertheless, this multi-faceted strategy allowed us to highlight matrix areas with the potential to support overall biodiversity as well as species of conservation concern. While our analysis did not aim to compare responses between these overlapping groups directly, we recognized that future analyses intended to explicitly distinguish differences among these categories might benefit from using mutually exclusive groups to enhance analytical clarity and interpretability.

Our results reveal limited spatial overlap among hotspot types—a trend consistent with previous studies on biodiversity prioritization (Orme et al. 2005, Grenyer et al. 2006, Ceballos and Ehrlich 2006, Jenkins et al. 2013). This suggests that different hotspot types reflect distinct ecological patterns and conservation opportunities, reinforcing the value of multi-criteria approaches in conservation planning (Marchese 2015). Building on this, previous studies have shown that incorporating functional and phylogenetic diversity helps capture species' ecological roles, evolutionary history, and contributions to ecosystem resilience (Cadotte et al. 2011, Brum et al. 2017, Stevens et al. 2019). Including these complementary dimensions could further refine hotspot identification within matrix areas, supporting conservation strategies that prioritize not only high species richness but also long-term ecological stability and evolutionary distinctiveness.

Our results indicate that hotspots based on threatened species capture the largest proportion of terrestrial mammal diversity within matrix areas compared to any other hotspot type. Despite their smaller spatial extent, these hotspots encompass over half of all extant terrestrial mammals, underscoring their disproportionate conservation value. This aligns with previous studies highlighting the importance of threat-based prioritization to efficiently direct conservation efforts toward species at the highest risk of extinction (Brooks et al. 2006, Allan et al. 2019, Wolff et al. 2023, Huais et al. 2025), particularly in human-modified landscapes where biodiversity loss is most acute (Newbold et al. 2015). While focusing on overall species richness remains valuable, our findings suggest that threatened species hotspots within matrix areas represent especially strategic targets for guiding restoration efforts, potentially yielding substantial conservation returns for terrestrial mammal diversity.

Although our analysis focused on terrestrial mammals, the framework we developed is readily transferable to other taxonomic groups. The growing availability of AOH maps (e.g., Nania et al. 2022, Lumbierres et al. 2022b, Neugarten et al. 2024) offers new opportunities to assess species richness within matrix areas across broader components of biodiversity. Applying this approach to additional taxa could reveal whether patterns of richness and conservation value within matrix areas are consistent across groups, supporting more integrative and taxonomically inclusive conservation strategies.

While our study underscores the importance of matrix areas for biodiversity conservation, the extent to which these areas actively support species persistence remains a critical knowledge gap. The ecological value of matrix areas depends fundamentally on their habitat structure, resource availability, and species-specific ecological requirements (Prevedello and Vieira 2010, Driscoll et al. 2013). Although species richness is frequently employed as a primary metric for biodiversity assessments (Marchese 2015, Di Marco et al. 2018a), richness alone does not necessarily reflect the functional capacity of matrix habitats to sustain viable populations or distinguish whether these habitats primarily serve as corridors facilitating species dispersal. Future research should thus complement our findings through detailed species-specific studies examining population viability, habitat selection, and dispersal patterns within matrix areas. Additionally, empirical validations leveraging independent observational datasets, such as citizen-science platforms (e.g., iNaturalist), could confirm the actual usage of matrix habitats by terrestrial mammals, providing critical evidence beyond predictions based solely on habitat suitability models (e.g., AOH maps).

We acknowledge an inherent methodological scale mismatch between fine-scale empirical studies, such as telemetry tracking, occupancy modelling, and camera trapping (e.g., Bassing et al. 2023), and broad-scale, global biodiversity analyses such as ours. Detailed studies typically provide nuanced insights into habitat selection, species-specific ecological responses, and fine-scale habitat dynamics, but are limited to smaller geographic extents or subsets of species. Conversely, global-scale biodiversity assessments typically rely on broader proxies, such as habitat suitability and species richness (e.g., Cohen and Jetz 2025), facilitating analyses across extensive spatial scales and diverse taxonomic groups. Given this mismatch, future efforts could strategically integrate insights from localized studies with global analyses to better understand species persistence in matrix areas, ultimately refining global conservation strategies.

A further potential limitation of our global analysis is that geographic variation in species diversity within matrix areas may partly reflect underlying natural variation in terrestrial mammal richness across regions. In this study, we intentionally did not standardize or control explicitly for these baseline regional differences, as our primary objective was to provide a straightforward global assessment of species richness within matrix areas. Future research could extend this framework by explicitly incorporating regional mammal richness patterns as covariates or through other standardization methods. Such an approach would provide additional insights into whether observed patterns in matrix areas differ meaningfully from general patterns of regional biodiversity.

As primary habitats continue to be lost or modified, species may increasingly depend on matrix areas for survival, making it necessary to reassess conservation priorities under dynamic environmental conditions (Powers and Jetz 2019). However, the extent to which matrix areas will serve as refugia or become further degraded remains uncertain. Predictive modeling approaches that integrate climate-driven habitat shifts, landscape connectivity, and land-use change could help identify matrix areas most likely to support species persistence under future scenarios (Carvalho et al. 2011, Bateman et al. 2013, Guisan et al. 2013, Powers and Jetz 2019). Such forward-looking strategies would enable more adaptive conservation efforts, allowing decision-makers to anticipate species responses to environmental change rather than relying solely on current biodiversity patterns.

Integrating matrix areas into conservation strategies aligns closely with global biodiversity targets, notably the Kunming-Montreal Global Biodiversity Framework's Target 2, which calls for effective restoration of degraded ecosystems to enhance biodiversity, ecological integrity, and connectivity (Maxwell et al. 2020, Allan et al. 2022, Obura 2023). Given that expanding formal protected areas faces substantial socioeconomic and political constraints (Watson et al. 2014, Schleicher et al. 2019, Sandbrook et al. 2023), matrix areas offer complementary opportunities to achieve biodiversity restoration targets (Kremen and Merenlender 2018, Galán-Acedo et al. 2019, Mokany et al. 2020). Conservation actions within matrix areas inherently involve balancing biodiversity conservation with human land-use demands, directly reflecting the ongoing debate between land-sharing approaches, which integrate biodiversity conservation within human-dominated landscapes, and land-sparing approaches, which intensify land use in some areas to allow strict biodiversity protection elsewhere (Phalan et al. 2011, Fischer et al. 2014, Grass et al. 2019, Williams et al. 2021). Critically, this perspective moves beyond the oversimplified dichotomy of habitat versus non-habitat, recognizing that multi-use and managed landscapes frequently retain significant ecological value and can actively sustain biodiversity (Tscharntke et al. 2005, Fischer et al. 2006, Kremen and Merenlender 2018). Our findings thus support an adaptive combination of land-sharing and land-sparing strategies, highlighting that even highly modified landscapes can retain substantial biodiversity, particularly when strategically managed or restored (Daily et al. 2001, 2003, Benton et al. 2003, Hole et al. 2005, Gardner et al. 2009, Arroyo-Rodríguez et al. 2020). This integrated perspective emphasizes context-specific management interventions that leverage the ecological realities and socioeconomic conditions of fragmented, multi-use systems (DeFries et al. 2007, Gardner et al. 2009, Perfecto and Vandermeer 2010, Kremen and Merenlender 2018, Mokany et al. 2020).

Our findings suggest that matrix areas—often overlooked in conservation planning—can support substantial terrestrial mammal diversity. By identifying species-rich matrix areas and mapping hotspots of species richness within them, our study expands the spatial scope of conservation opportunities beyond traditional habitat boundaries. As habitat loss and fragmentation continue to reshape ecosystems worldwide, prioritizing conservation action in matrix areas offers a practical and urgently needed strategy to complement existing conservation networks and help achieve global biodiversity targets. Integrating matrix areas into spatial planning, habitat management, and restoration will be essential for building resilient, connected landscapes that sustain biodiversity in a human-dominated world.

Chapter 5: Conclusions

In this dissertation, I investigated the role and conservation potential of the matrix for supporting terrestrial mammal diversity. Specifically, I quantified how matrix condition mediates the effects of habitat fragmentation on extinction risk, compared the predictive performance of alternative habitat intactness models (patch-matrix, continuum, and hybrid models), and identified hotspots of species richness within matrix areas. Despite long-standing conservation paradigms prioritizing primary habitats (Margules and Pressey 2000, Brooks et al. 2006, Gibson et al. 2011, Martin et al. 2012, Watson et al. 2018a, Di Marco et al. 2019), my findings clearly demonstrate the profound and indispensable ecological value of the matrix.

Matrix condition emerged as a key driver of extinction risk for terrestrial mammals globally, demonstrating greater predictive power than either habitat loss or habitat amount alone (Chapter 2). Importantly, the negative effects of habitat fragmentation intensified under conditions of high human pressure within the matrix, underscoring the critical need for conservation strategies that enhance matrix quality alongside traditional conservation approaches focused on primary habitats. Additionally, the hybrid habitat intactness model (Chapter 3) consistently outperformed traditional patch-matrix and continuum models in predicting extinction risk. By integrating continuous gradients of habitat quality with discrete habitat patches, the hybrid model better captures ecological complexity, representing an important methodological advancement for extinction risk assessments.

Moreover, my research provides a robust global assessment of species richness within the matrix, identifying previously unrecognized hotspots that may disproportionately represent global terrestrial mammal diversity (Chapter 4). Remarkably, these hotspots occupy only about 1% of Earth's terrestrial surface, yet potentially sustain over half of all terrestrial mammal species. Matrix areas with the highest conservation potential—identified by the overlap among hotspot types—are primarily concentrated in tropical strongholds such as parts of the Amazon Basin, the Colombian Tropical Andes, the Brazilian Atlantic Forest, and the Albertine Rift. This geographic concentration underscores the strategic value of targeted conservation in these areas, where action could yield disproportionately high returns for global biodiversity conservation. Furthermore, many of these areas with high conservation potential occur in landscapes facing intense human pressure yet currently lack adequate protection through formal PAs or recognition as OECMs, highlighting a critical conservation gap with substantial global implications.

Conservation implications

Given the current biodiversity crisis highlighted by recent landmark assessments (IPBES 2019, Obura 2023), effective conservation strategies must embrace multifunctional landscapes (Mokany et al. 2020). My work demonstrates that matrix areas can buffer species from extinction pressures and thus serve as valuable reservoirs of mammalian diversity (Chapters 2 and 3). These findings directly align with Target 2 of the Kunming-Montreal Global Biodiversity Framework, which aims to restore at least 30% of degraded terrestrial ecosystems by 2030 (Obura 2023). Because improving matrix quality can yield higher conservation returns than solely manipulating the size and configuration of remnant habitat patches (Donald and Evans 2006, Prugh et al. 2008, Franklin and Lindenmayer 2009, Ruffell et al. 2017, Ramírez-Delgado et al. 2022), targeting matrix areas identified as hotspots of species richness (Chapter 4) for restoration and improved management can represent an effective and efficient strategy to partially achieve this ambitious global restoration target, contributing to broader global biodiversity objectives. Moreover, the spatially explicit nature of my approach provides opportunities for further refinement to prioritize specific areas within these hotspots, enabling even more focused and effective conservation action.

Limitations and future directions

While this dissertation advances global understanding of the ecological role and conservation potential of the matrix for terrestrial mammals, certain methodological and conceptual limitations offer clear opportunities for future research.

The global-scale analyses presented in Chapters 2 and 3 primarily relied on metrics derived from human footprint data to predict extinction risk. While informative, these analyses excluded other pressures influencing extinction risk, such as overhunting (Ripple et al. 2016, Benítez-López et al. 2017), invasive species (Bellard et al. 2016, Doherty et al. 2016), disease outbreaks (Daszak et al. 2000, Scheele et al. 2019), climate change (Urban 2015, Foden et al. 2019), and pollution (Hernández et al. 2016, McCune et al. 2019). The omission of these factors likely increased uncertainty in extinction risk classifications, particularly for species at the greatest risk of extinction. Future extinction risk analyses could benefit from integrating these additional pressures, despite the methodological challenges associated with accurately mapping and quantifying them at global scales (Joppa et al. 2016, Di Marco et al. 2018b).

While changes in habitat intactness and human pressure levels have been explicitly considered (Chapters 2 and 3), extending these analyses to incorporate future dynamics, such as climate-driven changes in habitat quality, shifting species distributions, and evolving land-use pressures, also represents a compelling opportunity for future research. Incorporating dynamic scenario modeling, including climate change projections and future land-use scenarios, would allow researchers to better anticipate future shifts in extinction risk (Bateman et al. 2013, Powers and Jetz 2019).

The global hotspots of species richness identified in Chapter 4 relied primarily on global-scale spatial analyses. Although robust and informative in identifying broad patterns of mammalian richness within matrix areas, these global-scale assessments inherently cannot capture detailed ecological processes such as local population viability, demographic dynamics (e.g., survival and reproduction), species behavior, or fine-scale ecological interactions. As such, the identified hotspots do not directly provide evidence of demographic persistence or ecological stability of mammal populations within these areas. Empirical studies at finer ecological scales typically involve more nuanced data and methods, evaluating habitat quality along continuous gradients rather than simple patch-matrix distinctions, and focus on detailed habitat use and interactions among a limited set of species (e.g., Bommel et al. 2022, Koetke et al. 2025). Future research efforts should thus incorporate targeted empirical studies within selected hotspots, using high-resolution data and detailed ecological assessments. Such focused research would complement global findings, yielding deeper ecological insights that can refine conservation strategies and improve their effectiveness at local and regional scales.

While this dissertation focused on terrestrial mammals for both ecological and practical reasons, the scope could be expanded to other taxa in future work. At the time this research was initiated, mammals were the only vertebrate group for which globally consistent, high-resolution habitat data were available, making them the most suitable choice for large-scale analyses (Rondinini et al. 2011). Comparable high-resolution datasets are now available for birds (Lumbierres et al. 2022b), whose generally greater mobility and, in many cases, higher sensitivity to habitat edges (Schmiegelow et al. 1997, Batáry and Báldi 2004, Laurance et al.

2011, Bregman et al. 2014) could produce different spatial patterns and conservation priorities. Applying the analytical framework developed here to birds and other taxa would provide a valuable test of the generality of these results and could yield complementary insights for global conservation planning.

My global-scale analysis of species richness hotspots focused on taxonomic diversity (species richness), without incorporating functional or phylogenetic dimensions of biodiversity. Functional diversity, which captures ecological roles, resource-use strategies, and trait variation among species, and phylogenetic diversity, which reflects evolutionary distinctiveness, are increasingly recognized as critical for ecosystem resilience and adaptive capacity under environmental change (Cadotte et al. 2011, Brum et al. 2017). Integrating these additional biodiversity dimensions into hotspot analyses could provide more comprehensive ecological criteria, helping identify matrix areas that can not only support high numbers of species but also sustain critical ecosystem functions and evolutionary heritage.

Another limitation relates to practical considerations around restoration. Not all matrix areas identified as hotspots (Chapter 4) may realistically become suitable for all mammal species through targeted restoration efforts. Structural mismatches—such as attempting grassland restoration for forest-dependent species—as well as economic and logistical constraints, could limit the feasibility and effectiveness of restoration. Future analyses and management interventions should thus carefully evaluate restoration potential by explicitly considering species-specific habitat requirements alongside realistic socioeconomic and ecological constraints.

Additionally, my global assessment of species richness within matrix areas (Chapter 4) did not explicitly account for baseline regional variations in terrestrial mammal diversity. Thus, the patterns identified may partially reflect inherent regional differences rather than solely ecological responses to matrix conditions. Future global analyses would benefit from standardizing or explicitly controlling for regional richness patterns, thereby enhancing the interpretability and robustness of findings regarding the conservation potential of matrix areas at a global scale.

Translating the global-scale biodiversity insights from this dissertation into practical conservation outcomes demands bridging global analyses and local management actions. Global-scale conservation recommendations often face practical challenges in implementation at local and regional scales, where ecological, socioeconomic, governance, and political contexts differ widely (Knight et al. 2006, Watson et al. 2014, Di Minin and Toivonen 2015, Guerrero et al. 2018). Future research could help bridge this gap by establishing targeted, carefully designed adaptive management experiments within selected hotspots of species richness in matrix areas identified in this dissertation. Such adaptive experiments could aim to integrate ecological monitoring, socioeconomic assessments, and governance analyses, potentially involving approaches such as habitat restoration trials (Rey Benayas and Bullock 2012, Suding et al. 2015), agroforestry practices (Bhagwat et al. 2008, Jose 2009), sustainable land-use initiatives (Tscharntke et al. 2005, Kennedy et al. 2016), and community-based conservation interventions (Berkes 2007, Koricha and Jemal Adem 2024). Although logistically challenging, rigorous evaluation of these integrated management approaches could generate valuable, evidence-based insights to support effective, contextually adapted, and scalable biodiversity conservation actions in matrix areas globally.

The findings presented in this dissertation make a compelling case for revisiting and revising conservation frameworks globally, embracing matrix areas as critical ecological assets rather than marginal landscapes. Such integration would represent a transformative shift in global biodiversity conservation strategies, better reflecting ecological realities in the Anthropocene. As the global biodiversity crisis intensifies, recognizing and strategically managing matrix areas presents one of the most promising pathways for maintaining biodiversity, ecological connectivity, and ecosystem resilience in increasingly human-modified landscapes.

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Appendix A: Supplementary material for "Chapter 2: Matrix condition mediates the effects of habitat fragmentation on species extinction risk"

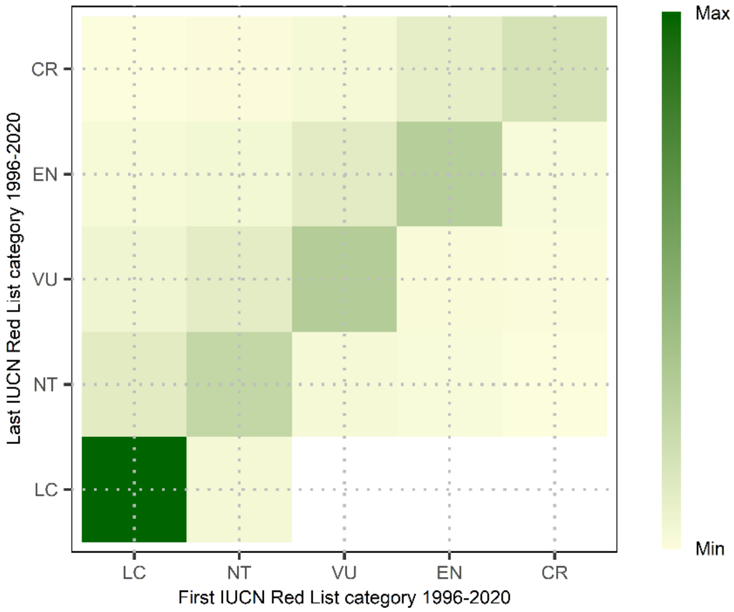

Figure A.1: Transition matrix of extinction risk categories for terrestrial mammals between 1996 and 2020. The plot shows the transition matrix of the first and last Red List category reported between 1996 and 2020. The colour scheme represents the relative frequency of individual species in each transition. Acronyms refer to the IUCN Red List categories, including Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). The relative frequency was arcsine square-root-transformed for visual purposes and to avoid variance instability when handling proportions close to zero.

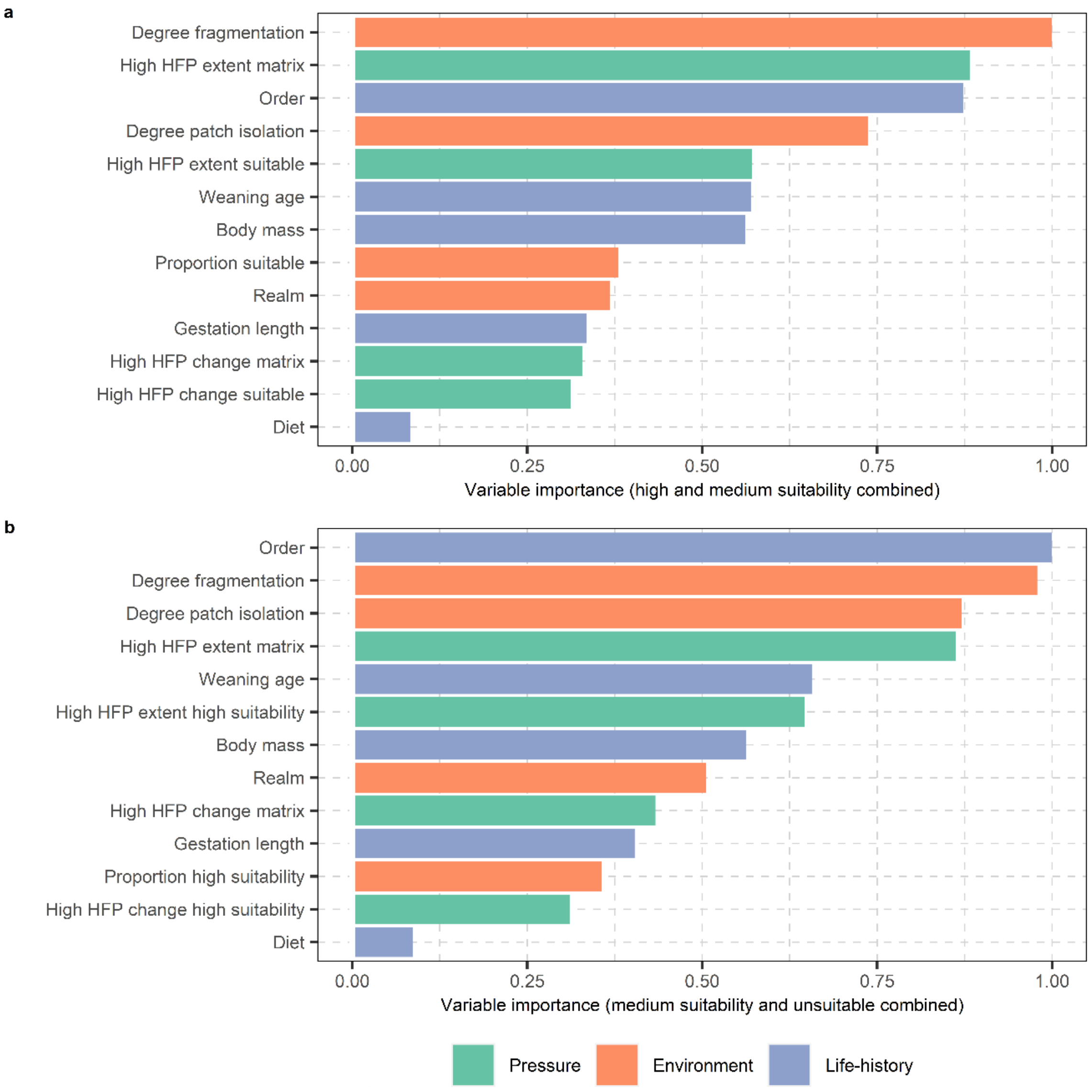

Figure A.2: Sensitivity analysis of selected variables for the prediction of extinction risk transitions in terrestrial mammals. Relative importance of each predictor when the extent of suitable habitat is represented by high and medium habitat suitability combined, and the extent of the matrix by unsuitable habitat alone (a). Relative importance of each predictor when the extent of suitable habitat is represented by high habitat suitability, and the extent of the matrix by medium habitat suitability and unsuitable habitat combined (b). Variables are colour-coded according to their broad class (human pressure, environment, and life-history). The description of each variable is given in Table 2.1 of the main manuscript. High levels of the human footprint (HFP) included values of 3 or above.

Table A.1: Cross-validation results of the Random Forest models for the prediction of extinction risk transitions in terrestrial mammals. *Cross-validation results when the extent of suitable habitat is represented by high and medium habitat suitability combined, and the extent of the matrix by unsuitable habitat alone. †Cross-validation results when the extent of suitable habitat is represented by high habitat suitability, and the extent of the matrix by medium habitat suitability and unsuitable habitat combined. The cross-validation was performed in terms of proportion of correctly classified species (accuracy), proportion of correctly classified high-risk species (sensitivity), proportion of correctly classified low-risk species (specificity), and the true skill statistic (TSS = sensitivity + specificity – 1).

Model	Accuracy (%)	Sensitivity (%)	Specificity (%)	TSS
Extinction risk transitions ~ High and medium suitability combined*	81.2	60.5	90.9	0.51
Extinction risk transitions ~ Medium suitability and unsuitable combined†	82.0	61.1	91.7	0.53

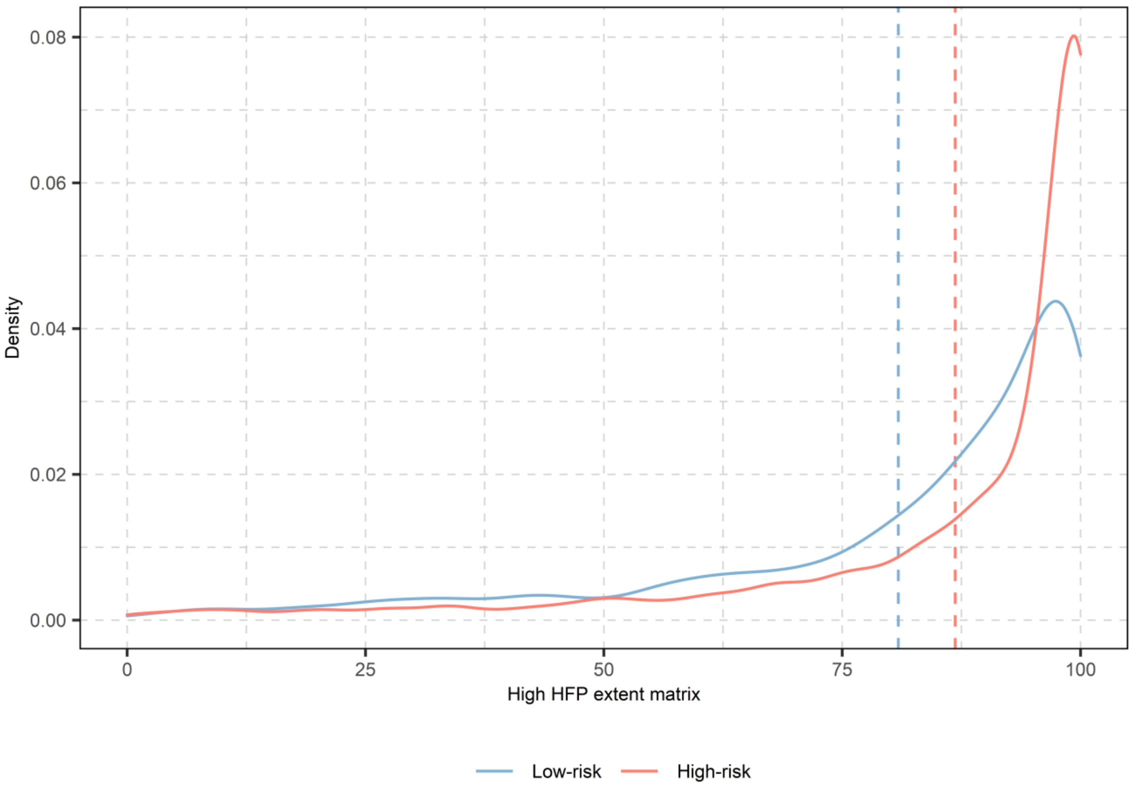

Figure A.3: Distribution of the matrix condition in low-risk and high-risk species at a global scale. The plot represents the frequency distribution of the extent of high human footprint values within the matrix of 4,329 species (68% low-risk species and 32% high-risk species). Species with ranges that did not overlap with the human footprint (2% of 4,426 terrestrial mammals in our sample) were excluded from the calculations. Blue and red lines refer to low-risk and high-risk species, as reported in legend. Dashed lines denote mean of distributions. High levels of the human footprint (HFP) included values of 3 or above.

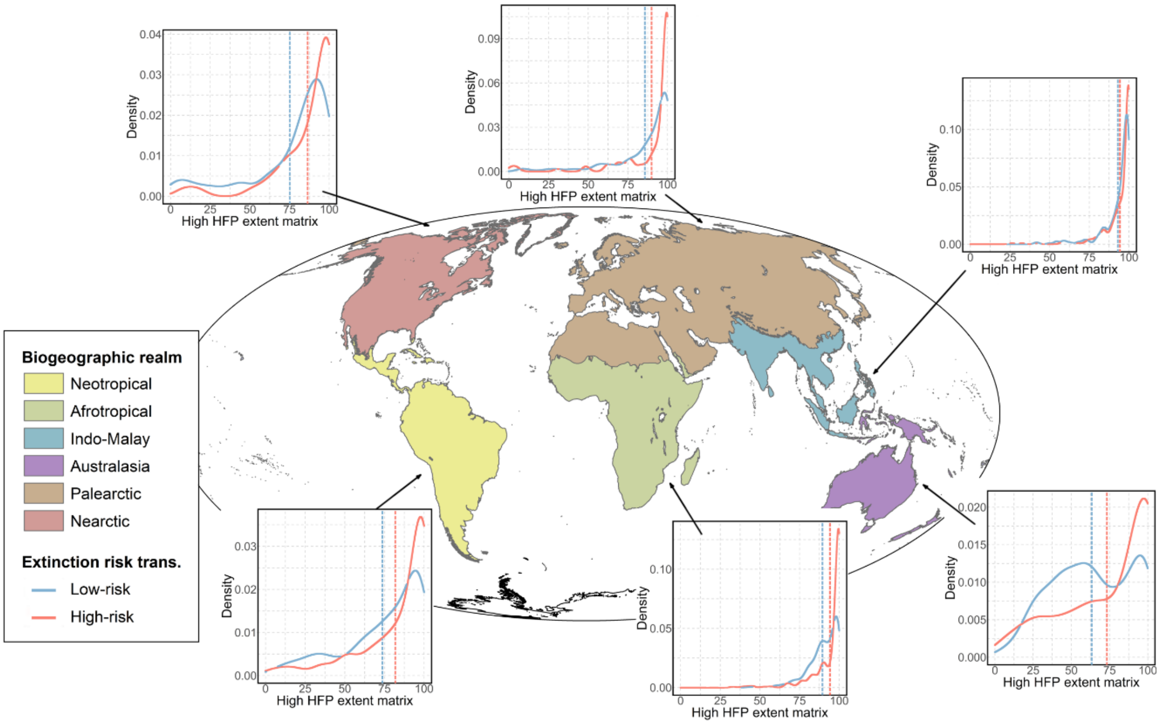

Figure A.4: Distribution of the matrix condition in low-risk and high-risk species at the scale of individual biogeographic realms. The plots represent the frequency distribution of the extent of high human footprint values within the matrix of 1.109 species in the Neotropical realm (68% low-risk species and 32% high-risk species), 990 species in the Afrotropical realm (65% low-risk species and 35% high-risk species), 596 species in the Indo-Malay realm (52% low-risk species and 48% high-risk species), 552 species in the Australasia realm (58% low-risk species and 42% high-risk species), 498 species in the Palearctic realm (79% low-risk species and 21% high-risk species), and 286 species in the Nearctic realm (83% low-risk species and 17% high-risk species). The Oceania realm included a total of 4 species only (17% low-risk species and 83% high-risk species), which are not depicted on the map. Species with ranges that overlapped with two or more realms (9% of 4,426 terrestrial mammals in our sample) were excluded from the calculations. Blue and red lines refer to low-risk and high-risk species, as reported in legend.

Dashed lines denote mean of distributions. High levels of the human footprint (HFP) included values of 3 or above.

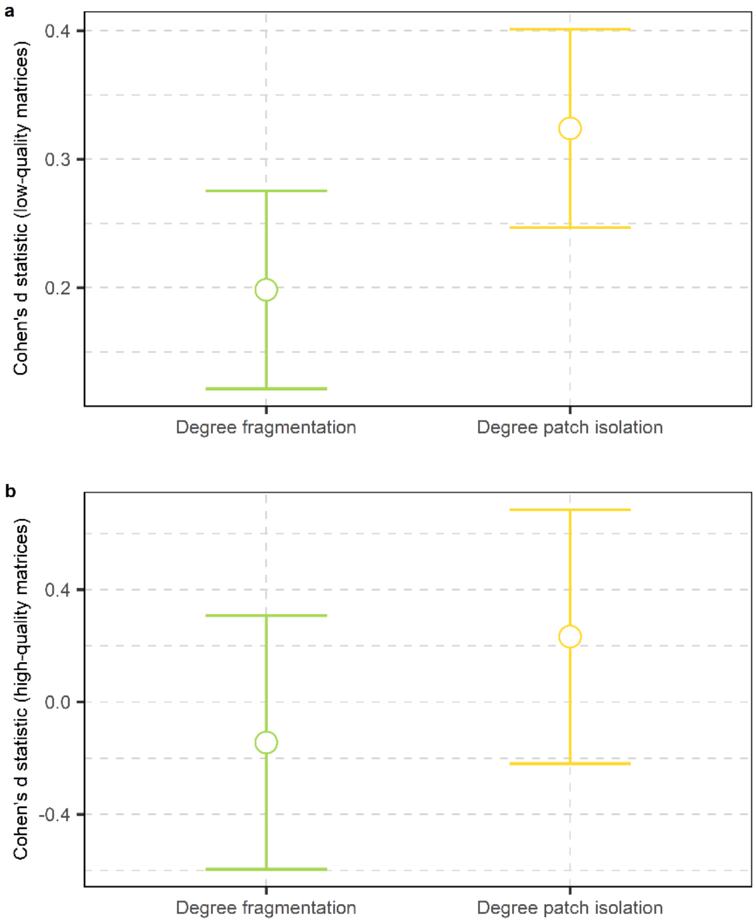

Figure A.5: Effect size (Cohen's d statistic) of the degree of habitat fragmentation and the degree of patch isolation between low-risk and high-risk species with a low-quality matrix and a high-quality matrix. Effect size of the degree of fragmentation and the degree of patch isolation between low-risk and high-risk species with a matrix of low-quality habitat (a). Effect size of the degree of fragmentation and the degree of patch isolation between low-risk and high-risk species with a matrix of high-quality habitat (b). Green and yellow points represent the effect sizes or the standardized difference of mean values (Cohen's d statistic) of the degree of fragmentation and the degree of patch isolation between low-risk and high-risk species, respectively. Error bars represent 95% confidence intervals for each effect size calculated. Low-quality matrices included species with proportions > 84.2% of the extent of their matrix overlapping with high human footprint values (*n* = 1,815 low-risk species and 1,027 high-risk species). High-quality matrices included species with proportions < 15.8% of the extent of their matrix overlapping with high human footprint values (*n* = 60 low-risk species and 29 high-risk species). High levels of the human footprint included values of 3 or above.

Appendix B: Supplementary material for "Chapter 3: Global comparison of habitat intactness models for predicting extinction risk for terrestrial mammals"

Supplementary methods B.1: Transformation of the human footprint (HFP) to habitat quality. Following previous work (Beyer et al. 2020), we transformed the HFP maps to quality using an exponential function ($w_i = exp(-\gamma HFP_i)$), such that habitat quality is 1 when the HFP is 0, and habitat quality is 20% when the HFP is 4. We applied this transformation based on the assumptions listed below: (i) A HFP value of 0 represents areas free of any human influence (i.e. the remaining wilderness areas on land) and the highest habitat quality; (ii) A HFP value of 4 represents areas of low human pressure, such as pasture lands with other human disturbances nearby (e.g., roads), and habitat quality should have declined to lower levels at this point; and (iii) HFP values above 8 represent areas of high human pressure levels, such as intensive agriculture and urbanized areas, and habitat quality should be approaching values of 0 at this point. We achieved these criteria using a value of $\gamma = 0.4023595$.

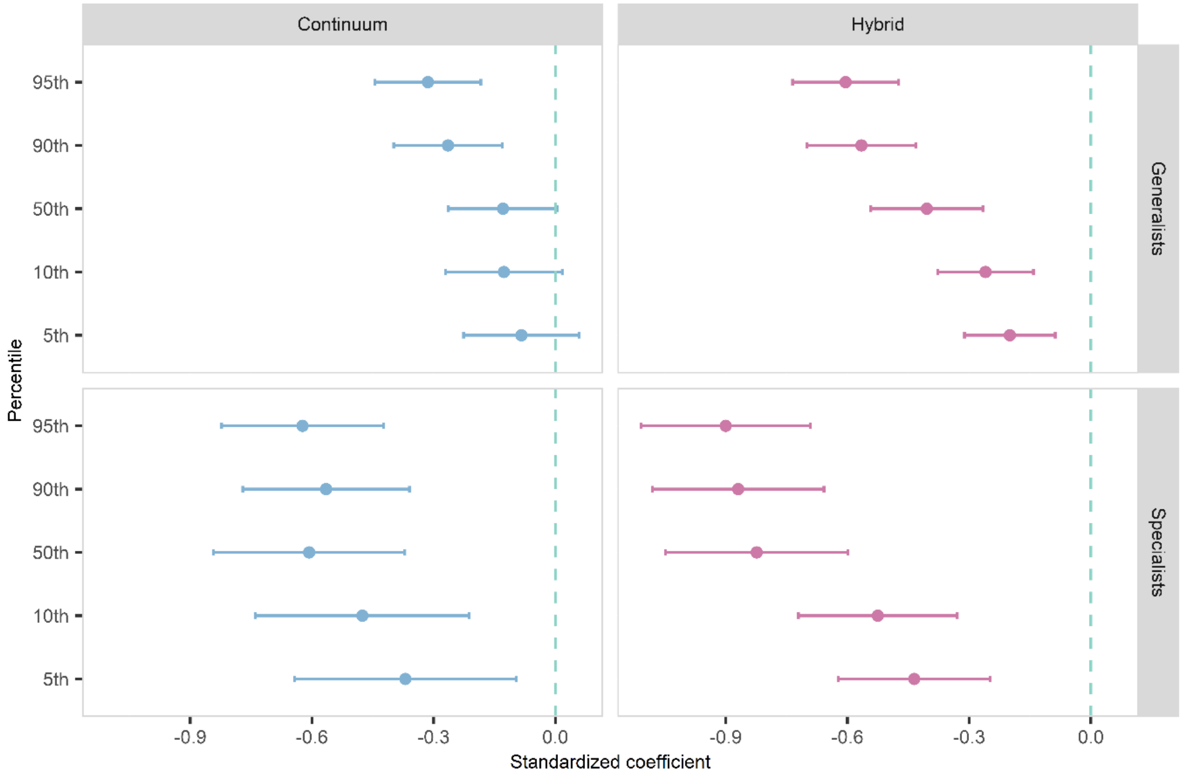

Figure B.1: Effects of the 5th, 10th, 50th, 90th, and 95th percentiles of the continuum and hybrid habitat intactness models on extinction risk for terrestrial mammals classified as habitat generalists and specialists. Each variable is colour-coded according to the habitat model (continuum or hybrid model) it represents. Effect sizes were estimated while holding other variables known to influence extinction risk (see Table 3.1) at their mean. All variables were standardized (z-transformed) before analysis to ensure comparable results. Error bars represent 95% confidence intervals. Confidence intervals not containing zero (dashed green line) indicate statistical significance.

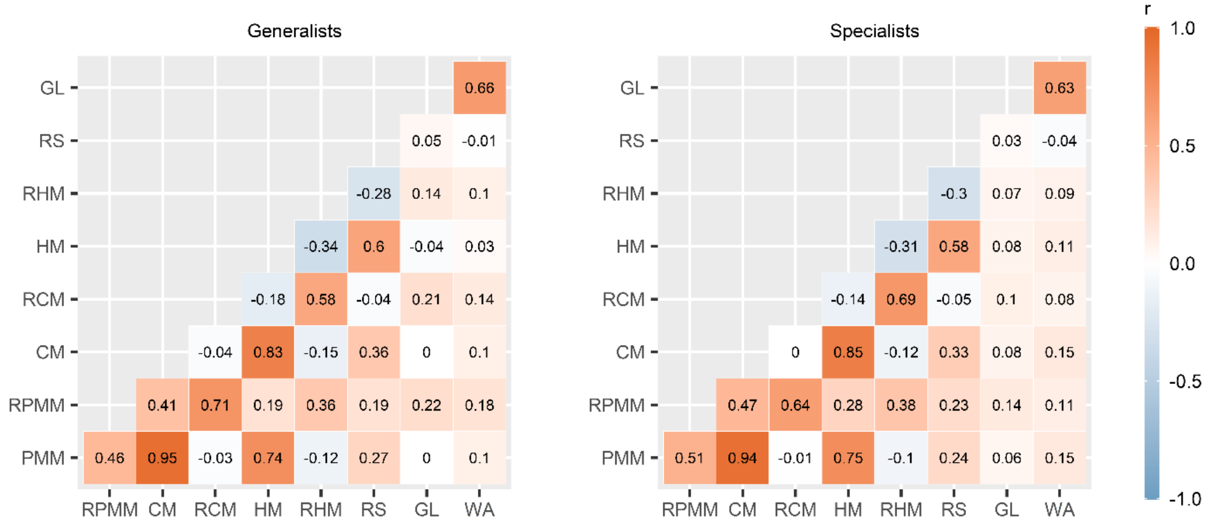

Figure B.2: Correlation between variables used to predict extinction risk for terrestrial mammals classified as habitat generalists and habitat specialists. Pearson's correlation coefficient (r) was used to quantify relationships between variables. Acronyms: patch-matrix model (PMM), reduction in the patch-matrix model (RPMM), continuum model (CM), reduction in the continuum model (RCM), hybrid model (HM), reduction in the hybrid model (RHM), range size (RS), gestation length (GL), and weaning age (WA). Detailed descriptions of these variables are provided in Table 3.1.

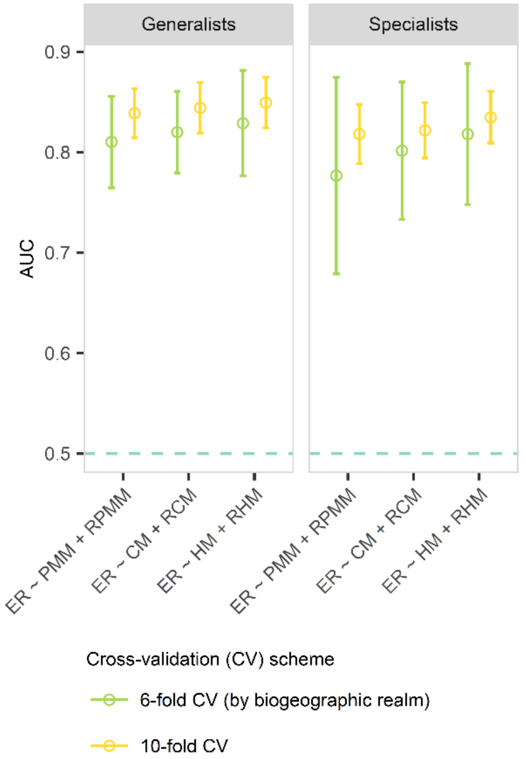

Figure B.3: Predictive performance of extinction risk models for both habitat generalists and habitat specialists as a function of three habitat intactness models and how they decrease over time. AUC values were estimated from mixed-effects logistic regression models using a spatially blocked cross-validation and a ten-fold cross-validation scheme (see Methods). AUCs above 0.5 (dashed green line) indicate that model performance is better than random chance. All extinction risk models accounted for the effects of other variables known to influence extinction risk (see Table 1). Error bars represent 95% confidence intervals. Acronyms: extinction risk model (ER), patch-matrix model (PMM), continuum model (CM), hybrid model (HM), reduction in the patch-matrix model (RPMM), reduction in the continuum model (RCM), and reduction in the hybrid model (RHM).

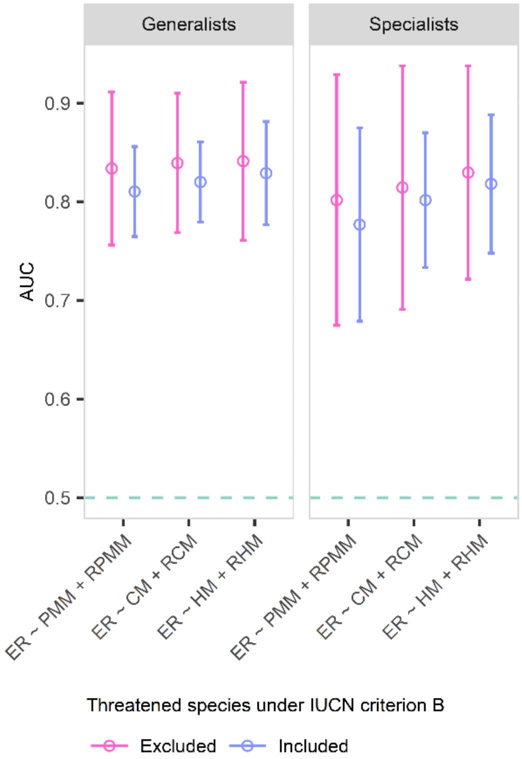

Figure B.4: Predictive performance of extinction risk models for both habitat generalists and habitat specialists as a function of three habitat intactness models and their temporal decline, before and after excluding threatened species assessed solely under IUCN Red List Criterion B. AUC values were estimated from mixed-effects logistic regression models using a spatially blocked cross-validation scheme (see Methods). AUCs above 0.5 (dashed green line) indicate that model performance is better than random chance. All extinction risk models accounted for the effects of other variables known to influence extinction risk (see Table 1). Error bars represent 95% confidence intervals**.** Acronyms: extinction risk model (ER), patch-matrix model (PMM), continuum model (CM), hybrid model (HM), reduction in the patch-matrix model (RPMM), reduction in the continuum model (RCM), and reduction in the hybrid model (RHM).

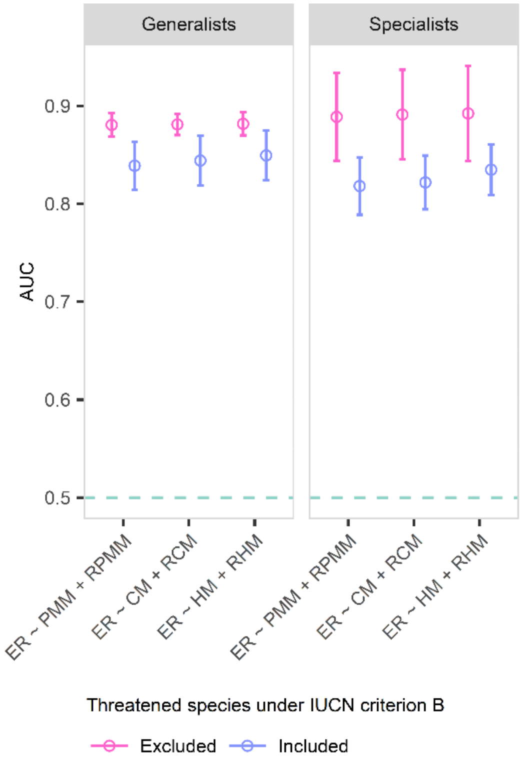

Figure B.5: Predictive performance of extinction risk models for both habitat generalists and habitat specialists as a function of three habitat intactness models and their decline over time, before and after excluding threatened species assessed solely under IUCN Red List Criterion B. AUC values were estimated from mixed-effects logistic regression models using a ten-fold cross-validation scheme (see Methods). AUCs above 0.5 (dashed green line) indicate that model performance is better than random chance. All extinction risk models accounted for the effects of other variables known to influence extinction risk (see Table 1). Error bars represent 95% confidence intervals. Acronyms: extinction risk model (ER), patch-matrix model (PMM), continuum model (CM), hybrid model (HM), reduction in the patch-matrix model (RPMM), reduction in the continuum model (RCM), and reduction in the hybrid model (RHM).

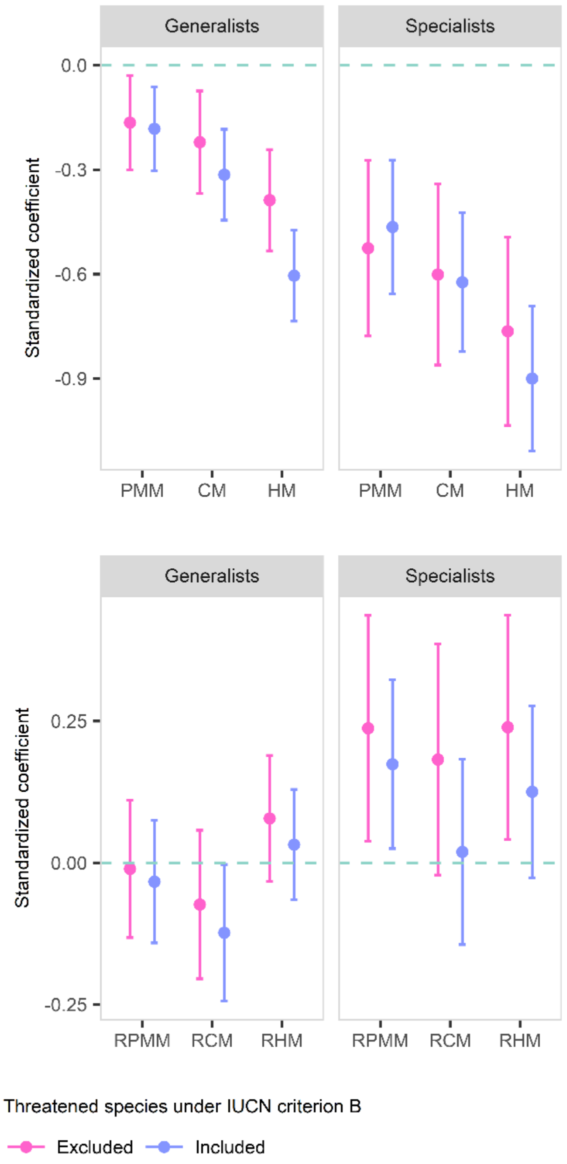

Figure B.6: Effects of three habitat intactness models and their decline over time on extinction risk for terrestrial mammals classified as habitat generalists and habitat specialists, before and after excluding threatened species assessed solely under IUCN Red List Criterion B. Effect sizes were estimated while holding other variables known to influence extinction risk (see Table 3.1) at their mean. All variables were standardized (z-transformed) before analysis to ensure comparable results. Error bars represent 95% confidence intervals. The statistical significance of the coefficients is indicated by the absence of overlap between their confidence intervals and zero (dashed green line). Acronyms: patch-matrix model (PMM), continuum model (CM), hybrid model (HM), reduction in the patch-matrix model (RPMM), reduction in the continuum model (RCM), and reduction in the hybrid model (RHM).

Appendix C: Supplementary material for “Chapter 4: Mapping the conservation potential of matrix habitats for terrestrial mammals”

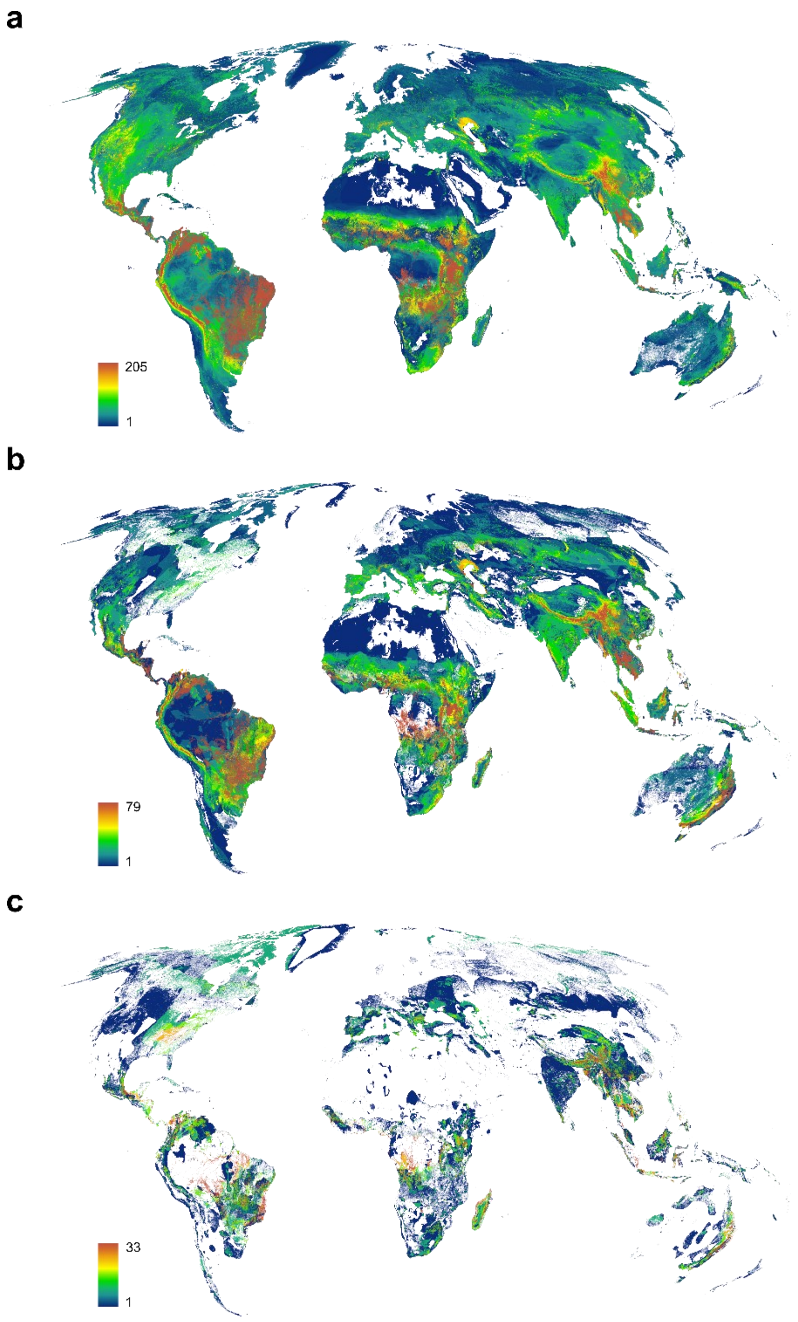

Figure C.1: Species richness in matrix areas for terrestrial mammals. Maps show species richness within matrix areas for all species (a), species with declining population trends (b), and species with threatened status (c). The dataset includes 5,439 species in the all-mammal group, 1,765 in the declining population trend group, and 1,212 in the threatened status group.

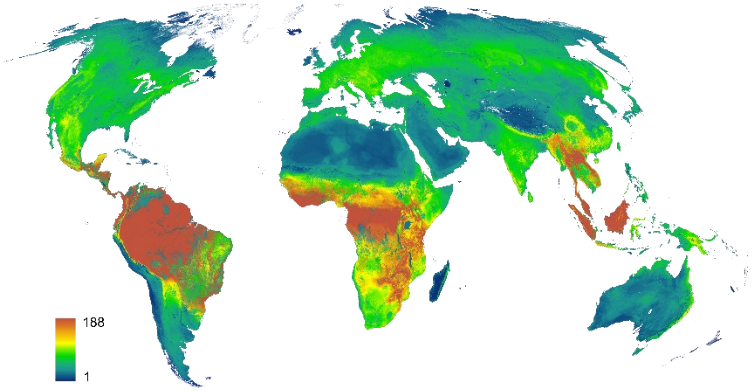

Figure C.2: Species richness in suitable habitats for terrestrial mammals. The map shows species richness within suitable habitats for the all-mammal group.

Table C.1: Geographic coverage and species representation of hotspot types under different hotspot definitions. The table includes the total area and number of species whose matrix area overlap with each hotspot type, based on two different thresholds: the top 2.5% and the top 10% of pixels with the highest richness values. Numbers in parentheses indicate the percentage of species-rich matrix areas (out of 15,922,965 km² globally) or the percentage of extant terrestrial mammal species (out of 5,808 species worldwide).

	2.5% criterion		10% criterion	
Hotspot type	Area (km²)	Number of species	Area (km²)	Number of species
All species	393,255 (2.5)	1,431 (24.6)	1,613,280 (10.1)	2,410 (41.5)

Declining trend	358,140 (2.2)	2,529 (43.5)	1,728,984 (10.9)	3,175 (54.7)
Threatened status	396,109 (2.5)	2,906 (50.0)	1,381,567 (8.7)	3,631 (62.5)
Total in all hotspots	864,005 (5.4)	3,078 (53.0)	2,852,778 (17.9)	3,792 (65.3)

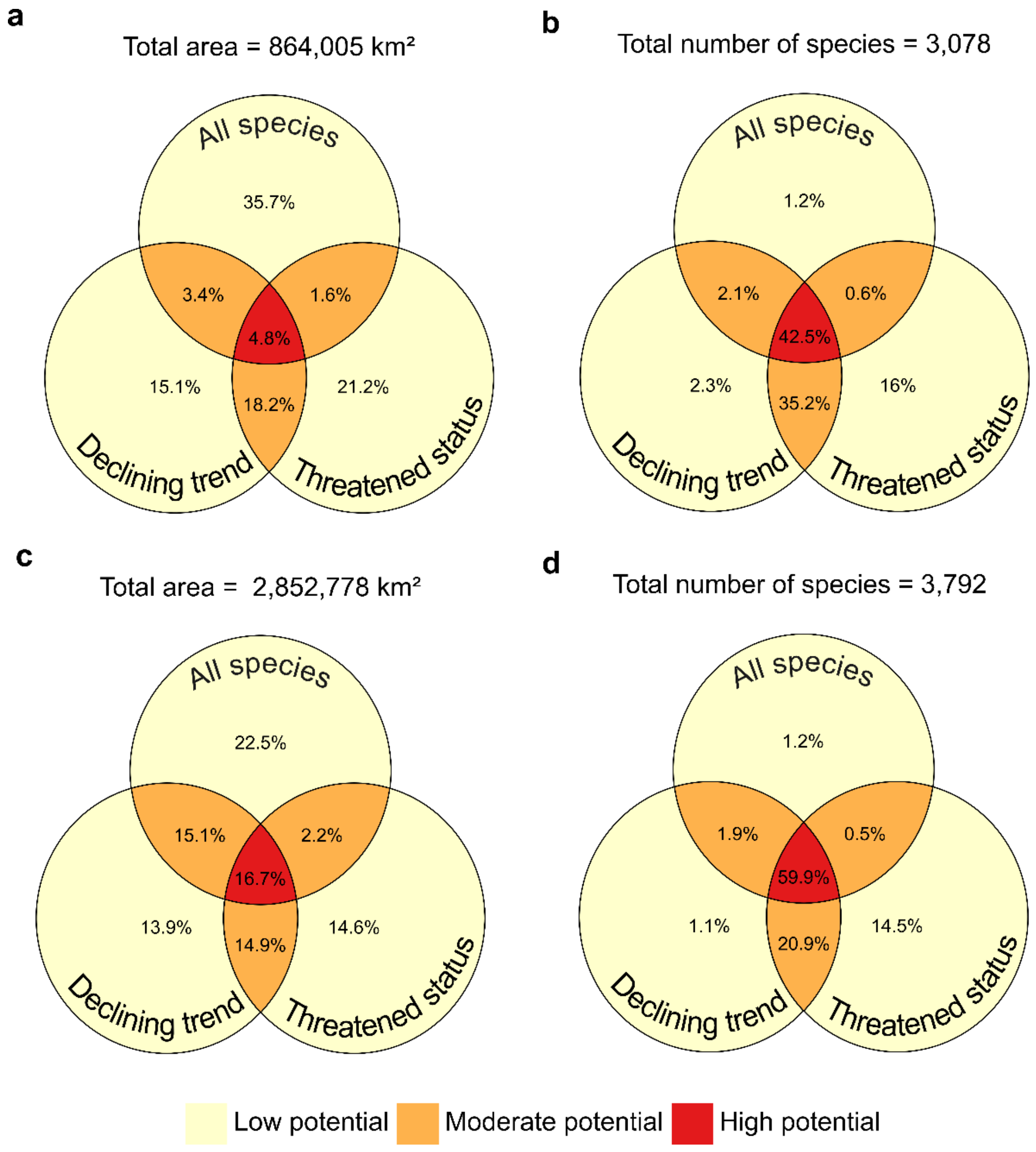

Figure C.3: Overlap of hotspot types and conservation potential in matrix areas across different hotspot definitions. Venn diagrams illustrate the spatial overlap of hotspot types (a, c) and species richness overlap across these hotspot types (b, d) under two different thresholds: the top 2.5% and the top 10% of pixels with the highest richness values for each species group (all mammals, mammals with declining population trends, and mammals with threatened status).

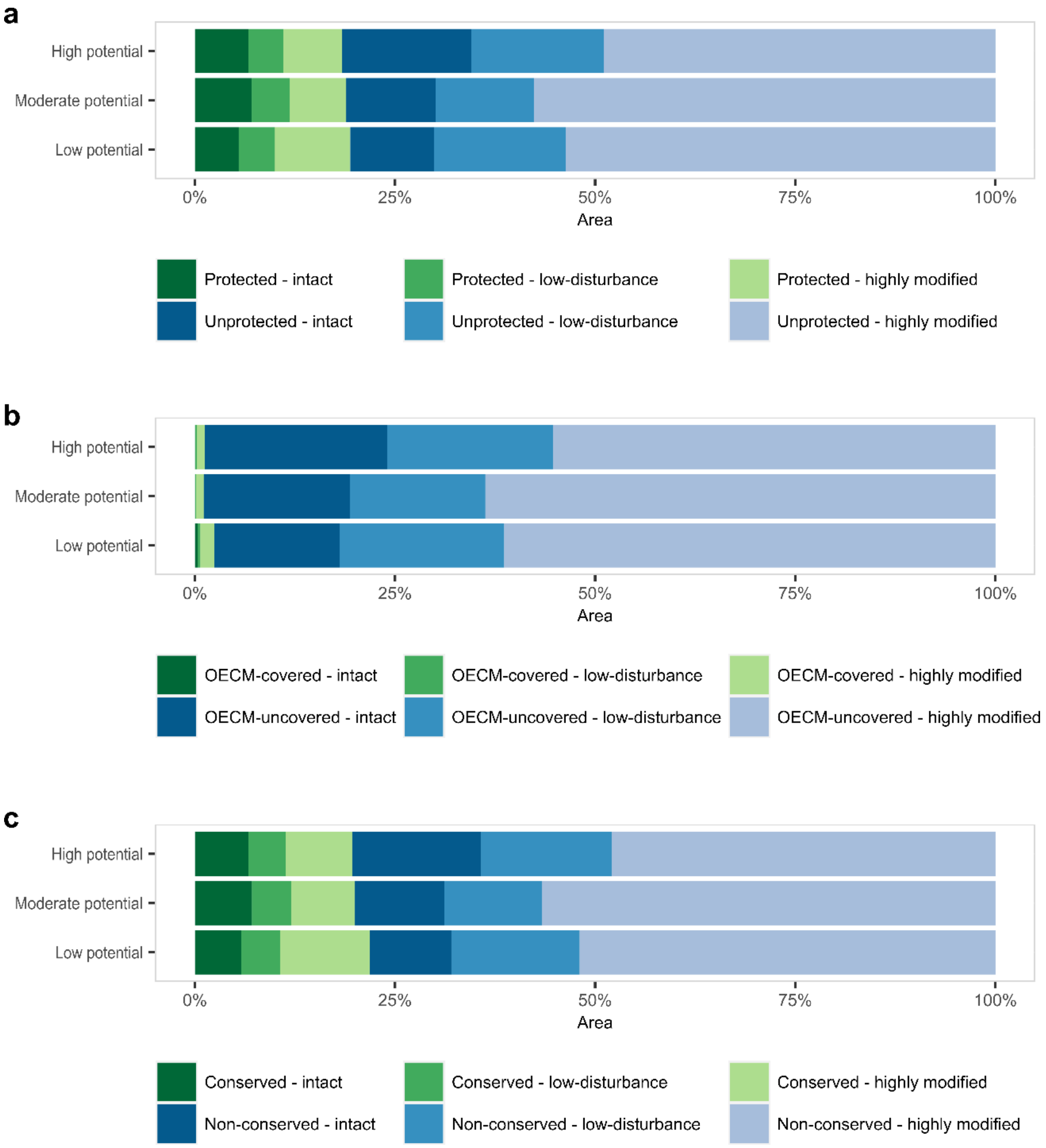

Figure C.4: Conservation status and human footprint within matrix areas with conservation potential. The figure shows the proportion of matrix hotspots classified as high-, moderate-, and low-priority that fall within protected areas (PAs) (a), other effective area-based conservation measures (OECMs) (b), and the combined coverage of PAs and OECMs (c). Bars are categorized by human footprint level: intact, low-disturbance, and highly modified.